

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2236

DECEMBER 17, 1965

A Review of the Mastotermitidae (Isoptera), Including a New Fossil Genus from Brazil¹

BY ALFRED E. EMERSON²

INTRODUCTION

The large majority of fossil termites are known only from fragmentary specimens, usually wings alone. These are often distorted or broken, and some of the veins may not be clearly discernible, particularly at the base of the wing near the humeral suture. Many characters of the species and higher taxonomic categories are lacking in the winged caste. The soldier caste, in particular, would add immensely to the accuracy of identification and relationship, but so far no sterile castes are known for any adequately classified fossil species of Tertiary or earlier periods.

Fossil termites are rare. The species are often known from single specimens only, dispersed in various paleontological collections around the world, and are seldom associated with the collections of modern termites. Thorough revisions based on first-hand study are virtually impossible for any specialist on the Isoptera, and a specialist on living termites has never collected a fossil termite personally. Many specimens were lost during the bombardments of cities during World War II, particularly in Hungary and Germany.

Fossil termites are usually collected and often studied by paleontologists who are not well acquainted with modern termites, and therefore

¹ The present investigation was supported by the National Science Foundation (Grant No. G-25146).

² Research Associate, Department of Entomology, the American Museum of Natural History, and Professor Emeritus of Zoology, the University of Chicago.

many mistakes in classification have been made even when significant characters are preserved. However, the descriptions and figures made by paleontologists provide basic information necessary for reclassification. Paleontologists have often been unaware of the degree of variation to be expected, particularly in the wing venation of a single species (see Fuller, 1919). An example of this type of error was made by A. Pongrácz (1928, p. 108) whose key characters are unreliable for both species and genera. At the same time, we would probably have no fossil termites available were it not for the active investigations of paleontologists, and the age of any fossil termite can be determined by the associated fauna and flora gathered and most often studied by paleontologists. Judgments concerning the paleoecology of the biota of any fossil stratum ultimately depend on the combined studies of numerous specialists and collectors from the fields of botany, zoology, paleontology, and geology. The present investigation is definitely a type that demands cooperation between specialists with different skills and interests through several decades.

Because of the paucity of material, its fragmentary preservation, and the errors of interpretation, one might question the value of the study of new fossils and the review of the earlier descriptions and classifications, particularly as no one can expect to avoid further errors, even with the most careful study and comparisons (see Ehrlich, 1964). Of the 17 fossil and one living species of termites reviewed in this article, I consider the taxonomic status and relationships of seven to be reasonably well understood, while 10 of the fossil species are questionable. Three of the fossil genera are based on fairly sound information, while four are considered questionable. However, I am convinced that an advance in our knowledge and understanding of the fossil remnants is possible, and that a solid basis of fact indicates a real order of evolution over millions of years of time. The data indicate former distributions, extinctions, and early origins of genera, one of which is still in existence (figs. 1-3). Phylogenetic relations of termite genera are fairly well understood, probably better than for most other groups of animals of comparative size. Theories of phylogenetic origins and dispersions based on studies of contemporary faunas can often be substantiated or refuted by a single fragmentary fossil. The homologies of fossil wings, however, must be correlated with other structures that are often not preserved in fossils (see Marks and Lawson, 1962; McKittrick, 1964, 1965). A total pattern is far more convincing than the homologies of structures such as wings alone. However, the known homologies between the cockroaches and the relict *Mastotermes darwiniensis* Froggatt indicate a high degree of reliability of interpretations based on the genetically complex wing.

Genetic homologies through long periods of geological time can be better comprehended by the study of fossil forms (Crampton, 1922, pls. 5-9; Tillyard, 1936, p. 655, figs. 1, 2). Homologies of the wing veins of termites and cockroaches provide circumstantial and phenotypic evidence of a degree of biochemical stability of the genetic system (Emerson, 1961, 1962), together with evidence of very slow (bradytelic) evolution since Permian times. Recently the biochemical basis of genetic homology has been indicated (McCarthy and Bolton, 1963; Hoyer, McCarthy, and Bolton, 1964), and this active field of investigation promises a rapid increase in our knowledge of the anticipated correlation between genetics, biochemistry, development, morphology, and systematics. The study of long-dead structures by the taxonomist provides crucial evidence of fundamental biological principles of vital concern to all aspects of modern biological research. For a critical survey of taxonomic axioms with several conclusions contrary to those expressed here, see Ehrlich (1964).

Collins (1925, p. 409) discussed the accuracy of generic determinations on the basis of single fossil wings of termites. He placed the species he described from Tennessee in *Mastotermes*, but this was later placed in the genus *Blattotermes* by Riek (1952, pp. 18, 19). From the forewings alone, I agree with Riek in the congeneric relations of the two fossil species from Tennessee and Queensland. It is quite possible, however, that these species might be classified in different but related genera if we had the entire structure of the imago and soldier castes preserved. The genus of fossil termites is usually based on a small number of characters and may be a wider concept than the genus of living termites incorporating many associated morphological, behavioral, and ecological characters. In many instances, the phylogenetic relationships of the fossils are still apparent, particularly in the primitive termites in which the wing venation has not been drastically reduced with the consequent loss of many taxonomic characters. The classification of the higher taxa of genus and family is founded on valid homologies that indicate genetic and evolutionary relationships. For example, the separation of *Blattotermes* from *Mastotermes* did not destroy the relationship of the included species within the Mastotermitidae, but only provided a nomenclature that symbolized a more primitive evolutionary stage for *Blattotermes* contrasted to *Mastotermes*. Likewise, if the known species of fossil *Mastotermes* were found to have other characters sufficient for the subdivision of the genus into two or more genera, or the genus *Miotermes* were synonymized with *Mastotermes*, the changes of generic names would simply indicate an expansion and refinement of our knowledge of the phylogenetic relations and evolutionary pathways of these termites.

Different authors have interpreted the homologies of the wing veins of termites in different ways, and have used different terms for the veins even when there is no great difference of opinion concerning their homologies within the Isoptera. The following discussion of the wing venation and wing structures of termites should help to avoid confusion for subsequent investigators and to point out the basic homologies even when the terminologies differ. The nomenclature of the wing veins and structures that I use is based on much comparative study of termites, but I have not carried on any researches on the related orders of Protorthoptera and Orthoptera. The living Blattaria, Isoptera, and Mantodea are classified as suborders within the order Dictyoptera by some authors (McKittrick, 1964, 1965), in which case the fossil Protorthoptera might be considered a suborder of the Dictyoptera that had its origin in late Paleozoic times more than 200 million years ago. In this article I follow Carpenter (personal communication) in retaining the orders Isoptera, Orthoptera, and Protorthoptera. If the Dictyoptera are considered to be a taxon, it would be of superordinal rank. My knowledge of the wing venation of these orders related to the Isoptera is based largely on the publications by Holmgren (1911), Comstock (1918), Crampton (1922), Martynov (1937), Rehn (1951), Snodgrass (1952), and personal correspondence with Dr. Frank Carpenter, the great specialist on fossil insects. When these investigators differ from one another, I am unable to make a critical judgment based on personal researches on orders other than the Isoptera.

The homologies of the wing veins (fig. 4) are based on the preceding homologies of the tracheation of the nymphal wing pads. Sufficient knowledge of the tracheal branches is available (Holmgren, 1911; Comstock, 1918; Fuller, 1919; Tillyard, 1931) to allow a fair degree of accuracy in determining the homologies of the wing veins of both fossil and recent termites. The evolutionary trends are toward reduction, so that the primitive termites have more veins and more branches than the derivative genera. Generic characters are more easily observable in the wings of primitive species, while the advanced genera seldom have sufficient characters in the wings alone to allow generic separation. It is unwise to name genera based on fossil wings of advanced types when the systematics and phylogeny cannot be ascertained. For example, *Architermes simplex* Haupt (1956, pp. 128, 129) is a species that cannot be assigned readily to family, let alone genus.

TERMS USED FOR WING STRUCTURES AND VENATION

COSTAL MARGIN (C): In termites, the thickening of the costal border is not preceded by a tracheal branch. If a tracheal branch of the costa is

present at all, it is greatly reduced and is not the foundation for a true vein visible beyond the humeral suture of either the forewing or the hind wing. My term equals the costa of Desneux (1904a, fig. 3), Holmgren (1911, p. 22, text fig. 2), and Snodgrass (1952, fig. 84).

SUBCOSTA (Sc): This vein is preceded by a tracheal branch in termites. It is either short in the forewing of primitive termites or absent from derivative genera. It may extend more than half of the length of the hind wing, with a series of short superior veinlets, or may be short without veinlets. It may be single or branched in termites, but is not so long as it is in the Protorthoptera. The subcosta arises separately from the radius both in the wing scale and beyond the humeral suture of the forewing and hind wing. As I use the term, the subcosta is homologous with the costa of Silvestri (1909, figs. 11, 16); the subcosta of Desneux (1904a, p. 281, fig. 3; 1904b, p. 10, fig. 2), Holmgren (1911, p. 22, text fig. 2), Comstock (1918, p. 136, fig. 128), Tillyard (1931, pp. 374, 377, figs. 1-6), and Snodgrass (1952, pp. 317, 338, fig. 84); and the post-costa (Pst.-C) of Fuller (1919, p. 29). Comstock (1918, p. 138, figs. 128, 131) considered the main branch of the subcosta to be Sc_2 , but I doubt whether the branched or unbranched vein is sufficiently fixed to be worthy of giving separate designations to the branches.

FIRST RADIUS (R_1): This vein is present in the forewing and some hind wings of numerous primitive termites, but is in some instances absent from the hind wing when it is present in the forewing. It may be separated from the other branches of the radius beyond the humeral suture, or it may be joined with the second and third radius. When present, it is preceded by a tracheal branch of the radius. Although more stable than the second and third radius, there is a great variation in its occurrence within the same genus. It is longer than the subcosta and occasionally may be branched. It is usually a short vein, but in some individuals of the same species it may extend more than half of the length of the wing before joining the costal border. In the fossil wings in which the base may not be flattened out, the first radius is sometimes erroneously identified with the subcosta, but in other cases the homology of the vein may not be in doubt although the vein may be given a different term. When the radius has a single vein at the humeral suture of the hind wing in addition to the radial sector, it is not always possible to be sure whether it is the first radius or the second plus third radius. In some cases the first radius is reduced. As I use the term "first radius," the vein is probably homologous with the subcosta of Silvestri (1909, figs. 9, 11, 16); questionably with the subcosta of Riek (1952, fig. 1); with the radius of Desneux (1904a, p. 281, fig. 3), and of Holmgren (1911, p. 22); with the first

radius of Desneux (1904b, fig. 2), Comstock (1918, p. 136, figs. 128, 132), Tillyard (1926, fig. H3; 1931, p. 374, figs. 1-6), and Emerson (1933, figs. 14, 31, 32); with the praeradius (portion) of Martynov (1937, fig. 7); and with the radius (portion) of Snodgrass (1952, pp. 317, 338, fig. 84).

SECOND RADIUS (R_2): This vein is sometimes present in primitive wings, but is often more variable in the forewing of both species and genera than the first radius. It may emerge from the humeral suture separately from the first and third radius, but it is also often joined with these branches beyond the suture, particularly with the third radius (R_{2+3}). So far as I know, neither the second nor third radius is ever joined with the radial sector beyond the humeral suture, although they have been confused by some authors with the first superior branch of the radial sector. As I use the term, the second radius is homologous with a portion of the radius or radial sector of Holmgren (1911, p. 22); questionably with the subcosta of S. Pongrácz (1917, fig. 1), and of Riek (1952, fig. 1); with the second radius of Comstock (1918, p. 136, fig. 128), Tillyard (1926, fig. H3; 1931, p. 374, figs. 1-6), and Emerson (1933, figs. 14, 15, 31, 32); and with the praeradius (portion) of Martynov (1937, fig. 7).

THIRD RADIUS (R_3): This vein is present in some cases as a separate unbranched vein beyond the humeral suture in primitive wings, or may appear fused with the second radius, or as a branch of the second plus third radius. It also may be absent from primitive wings and should not be relied on as a specific or generic character of rigid stability. As I use the term, it is homologous with a portion of the radius or radial sector of Holmgren (1911, p. 22, text figs. 2, 3) and the third radius of Comstock (1918, p. 136, fig. 128), Tillyard (1926, fig. H3; 1931, p. 374, figs. 1-6), and Emerson (1933, figs. 14, 15, 31, 32).

RADIAL SECTOR (Rs): This is the major vein in the termite wing that gives rigidity for the function of flight, often serving together with the thickened costal margin and other associated veins. In primitive wings the radial sector has a variable number of superior branches that join the costal border, and it may also have a few inferior branches, particularly in the Hodotermitinae. In the advanced families, the radial sector is unbranched. It reaches close to the tip of the wing in all termites. The radial sector and its branches (if present) are preceded by tracheal branches, and its position and branching in the wing in relation to the costal border and to the media may be diagnostic of genera and related groups of genera. There is no reason to suppose that the vein originated through the fusion of a definitive fourth and fifth branch of the radius (see Comstock, 1918; Tillyard, 1931, p. 378), so it is best to drop the term

"fourth plus fifth radius" (R_{4+5}). As I use the term "radial sector," it is homologous with the radius of many authors, including Desneux (1904b, fig. 2), Fuller (1919, p. 29), Collins (1925, fig. 2), and Martynov (1937, fig. 7); with the fourth plus fifth radius (R_{4+5}) of Comstock (1918, figs. 126, 128, 132, 134), Tillyard (1931, p. 374, figs. 1-6), and Emerson (1933, figs. 4, 14, 15, 32); and a portion of the radius of Snodgrass (1952, pp. 317, 338, fig. 84). Comstock (1918) used the term "radial sector" for the basal stem of the radius that branches into R_2 , R_3 , R_4 , and R_5 in his hypothetical primitive wing.

MEDIA (M): This vein and its preceding tracheal branch are present in nearly all termites, but in a few genera the vein is short and fuses with the radial sector or the cubitus beyond the humeral suture, and in a few individuals (variable in the same species) it is absent or fused with other veins in the adult wing. In nearly all cases, the media is joined with the radial sector for a short distance beyond the humeral suture in the hind wing and in some cases with the cubitus in the forewing, but there are a few variations and exceptions (i.e., *Prorhinotermes*). The media is joined to the base of the radial sector in the hind wing of the cockroach, *Periplaneta americana* (Snodgrass, 1952, fig. 84), an indication of a very ancient character ancestral to the Isoptera. The position of the media in relation to the radial sector and to the cubitus, together with the points at which its branches reach the tip of the wing and inner border, may be diagnostic of certain genera or groups of genera of termites. Also the relative thickening or strength of the media is an important character in some genera of the Kalotermitidae (Krishna, 1961, p. 390). However, the number and position of its branches are often variable within the same species, and several species and genera have been mistakenly separated on the basis of the variation of the branching. My term is homologous with the media or mediana of nearly all authors. Tillyard (1931, p. 374) pointed out that there is general agreement on the homology and nomenclature only for the media among the veins of the termite wing. Fuller (1919) called the vein both the "media" and "pseudimedia."

ANTERIOR CUBITUS (CuA) OR CUBITUS (Cu): This vein is always present in both wings of termites and has numerous and variable numbers of inferior branches that reach to the tip or the inner border of the wing. The relative length of the cubitus and its position in relation to the media may have some diagnostic value in the separation of species and higher categories, but the variation is great. The assumption of rigid invariance has resulted in errors of classification. In the Mastotermitidae, the trachea preceding the vein branches near the base into the anterior and posterior cubitus, but the posterior cubitus is regressed or atrophied

in the other families of termites. My term is homologous with the cubitus of nearly all authors. Tillyard (1931, pp. 374, 378, 379, figs. 1-4) and Grassé (1949, fig. 99) referred to the vein as the first cubitus (Cu_1).

POSTERIOR CUBITUS (CuP): Dr. Frank Carpenter (personal communication) has informed me that the terms "anterior" and "posterior cubitus" have been well established in recent literature dealing with other orders. Holmgren (1911, p. 25) stated that this is a false vein and is not preceded by a tracheal branch. Tillyard (1931, pp. 374, 378-380, figs. 1-4) demonstrated a tracheal branch in *Mastotermes* that branches off the base of the cubitus and may or may not be branched near its tip. It is weaker than the first anal in the hind wing of the Mastotermitidae. A very short, reduced, posterior cubitus is present in the forewing of the Mastotermitidae. As I use the term, the posterior cubitus is homologous with the first anal (A_1) of Desneux (1904a, p. 281, fig. 3; 1904b, fig. 2), Silvestri (1909, fig. 16), and Comstock (1918, fig. 129); the "1:e analis" of Holmgren (1911, p. 25); the CuP of Martynov (1937, fig. 7); one of the postcubitals of Snodgrass (1952, pp. 317, 338, fig. 84); and the second cubitus (Cu_2) of Tillyard (1931, pp. 378-380, figs. 1-6) and Grassé (1949, p. 99). I follow the suggestion of Dr. Frank Carpenter in using the term "posterior cubitus," because it has become the better-established name in recent literature dealing with fossil orders related to the termites.

FIRST ANAL (A_1 OR A): This is a strong vein with numerous short inferior branches in the hind wing of the Mastotermitidae, in which family it is as long as the anal fold. I believe it is homologous with the short, reduced, anal vein (A) present in many primitive and somewhat primitive families and genera of termites that lack the anal lobe of the Mastotermitidae, the Orthoptera, and the Protorthoptera. Martynov (1937) showed that a reticulum in the scale of the forewing is homologous with the first anal of the hind wing. My term is homologous with the second anal (A_2) of Desneux (1904a, p. 281, fig. 3; 1904b, fig. 2), Silvestri (1909, fig. 16), and Comstock (1918, fig. 129); *Analis im Analfeld* of Holmgren (1911, p. 23); anal region (An) of Martynov (1937, fig. 7); the first anal (A_1) of Tillyard (1931, p. 379, figs. 1-4, 6) and Grassé (1949, fig. 99); and the Cu_{1b} of Tillyard (1926, fig. H3). I agree with the discussion by Tillyard (1931, 1936) of the homologies of this vein and its preceding tracheal branches.

ANAL FIELD (Af): This term refers to numerous branched veins in the anal lobe of the hind wing of the Mastotermitidae that are not present in other termites except possibly in a reduced condition within the scale of the other families of Isoptera. Tillyard (1931) showed that tracheal stems arise either separated or fused at the base and often branch in variable

patterns in the peripheral portions of the nymphal wing pads of the forewings and hind wings. Snodgrass (1952, p. 317) stated that tracheal branches precede these veins in the cockroach. The tracheae of the anal field are present but reduced in the forewing pad of the nymph of *Mastotermes*, but the veins are vestigial in or absent from the mature forewing of *Mastotermes* and in both wings of the other families of termites. My term is homologous with the anal (A) of Desneux (1904b, fig. 2) and Silvestri (1909, fig. 16); with the *Postanalfeld* of Holmgren (1911, pp. 22, 23, 24, 25); with the third anal of Comstock (1918, fig. 129); with the first, second, and third anal of Tillyard (1926, fig. H3; 1931, pp. 574, 579, figs. 1, 2, 3, 4); with the jugal veins of Martynov (1937, fig. 106); and the vannal veins of Snodgrass (1952, p. 317).

ANAL FOLD: This is a distinctive fold in the hind wing of the Mastotermitidae, Protorthoptera, and Orthoptera. It is situated between the first anal vein and the anal field in the Mastotermitidae and in the fossil cockroach, *Pycnoblattina*, from the Permian of Kansas, and separates the anal lobe from the main part of the wing. It is reduced in or absent from the other families of termites that lack the anal lobe. It is homologous with the axillary furrow of Comstock (1918, p. 138); Pl of Martynov (1937, fig. 10b); the vena dividens of the hind wing of Tillyard (1931, p. 379); and the vannal fold of Snodgrass (1952, pp. 317, 339, fig. 84). Tillyard (1931) believed that the anal fold forms along the first branch of the first anal vein ("second anal") of the hind wing of *Mastotermes*, and that the vena dividens forms along the posterior cubitus ("Cu₂") in the forewing. The anal fold may be between the cubitus and the first anal vein in most cockroaches (see Snodgrass, 1952, fig. 84), but Tillyard (1936, p. 655) showed the relationships of this character in cockroaches and termites.

ANAL LOBE: This term is used by most authors for the distinctive fan-like portion of the hind wing containing the veins of the anal field (A). The anal lobe is well developed, large, and unfolded in the Mastotermitidae, but is greatly reduced in the forewing of the Mastotermitidae and the hind wing of all the other families of Isoptera. My use of the term is homologous with the anal lobe of Tillyard (1931, p. 383), the jugal lobe of Martynov (1937, figs. 3, 7), and the vannus of Snodgrass (1952, pp. 316, 339, fig. 84). A jugal region and jugal fold are also present in the cockroaches (Snodgrass, 1952, p. 338, fig. 84), but are absent from the termites. Consequently I think Martynov's jugal lobe is a misnomer.

BASAL STRIPE: This is a sclerotized region from which the veins of the anal field arise in the Mastotermitidae. A sclerite is also present at the base of the anal vein (A) in the hind wing of other primitive termites that may be a fusion of the basal stripe with another sclerite (Emerson, 1933,

figs. 15, 32). The basal stripe is termed "juch" by Martynov (1937, fig. 10b) and a portion is labeled "ant" in the same figure. Tillyard (1931, p. 383, fig. 6) and Grassé (1949, fig. 99) call it the "third axillary" (Ax_3) in *Mastotermes*. I am not sure whether the third axillary of the cockroach (Snodgrass, 1952, fig. 84) is homologous, or what the homologies may be in all groups of termites and their related orders.

ARCHIDICTION: This term was used by Tillyard (1931, p. 389) and Rieck (1952, p. 17) for the complex network or reticulum of irregular veinlets between the veins in the apical three-fourths of both wings, including the anal lobe. The archidiction is characteristic of the Mastotermitidae and Hodotermitidae, but the individual veinlets cannot be homologized with one another or with the named cross veins of other insect orders.

HUMERAL SUTURE: This breakage suture at the base of both forewing and hind wing is diagnostic of all termites and is absent from the Protorhoptera, Orthoptera, and other orders of insects. Following the colonizing flight, the four wings are broken off along the humeral sutures, leaving the bases of the wings or scales attached to the thorax. The humeral suture is more distinctive in the forewing of primitive termites than in the hind wing, but it is present in both. Comstock (1918) named the breakage line the humeral suture, but stated that it is absent from the hind wings of some genera. Tillyard (1931, pp. 384-386) discussed dealation in *Mastotermes*. He did not regard the breakage line of the hind wing as a true suture, but I do regard the weak line in primitive termites as a suture or the beginning of an evolution of a suture. Tillyard (1936, p. 655, fig. 2) referred to the humeral suture and figures it in the hind wing of *Mastotermes darwiniensis* Froggatt. The curvature of the humeral suture differs in degree and angularity and may distinguish some closely related genera. The more primitive genera have a comparatively slightly curved humeral suture in contrast to the strongly curved and more angular humeral suture of the derivative genera (Emerson, 1933, 1962). The veins that emerge beyond the humeral suture are often important characters of genera, particularly in the primitive families.

WING SCALE: This is the basal part of the wing limited by the humeral suture and remaining on the imago or primary reproductive caste after the main portion of the wing is shed. In primitive termites, the scale of the forewing is much larger than that of the hind wing and usually overlaps the base of the scale of the hind wing or the hind border of the mesonotum. In the more advanced termites, the scale of the hind wing is more equal in size to that of the forewing, but it is still somewhat smaller. There is no doubt that the relative size of the forewing scale has been

analogously reduced several times in the evolution of different groups of termites. The relative sizes of the scales of the forewing and hind wing are definitive characters of some families and of some genera within families. The term as I use it is homologous with the scapular shield of Foggatt (1913) and Comstock (1918), and the wing stump of Fuller (1919, p. 30). Fuller used the term "lamina" for the deciduous apical portion or main portion of the wing. Tillyard (1931) and Riek (1952, p. 19) used the term "clavus" for the anal portion of the scale.

ORDER ?PROTORTHOPTERA

Dr. Frank Carpenter (personal communication) has informed me that, in the "Treatise on Invertebrate Palaeontology," he is now planning to assign the fossil orthopteroid orders formerly separated into the Proto-blattoidea and Paraplecoptera to a single order Protorthoptera. I am following his suggestion, which is based on long and wide experience with Paleozoic fossil insects.

FAMILY URALOTERMITIDAE ZALESSKY

- = *Uralotermidae* [sic] ZALESSKY, 1939, pp. 53, 80.
- = *Uralotermidae*: SNYDER, 1949, p. 352.
- = *Uralotermidae*: EMERSON, 1955, pp. 506, 507.

Zalessky assigned the Uralotermitidae to the order Isoptera and the taxon has been considered by numerous authors to be a representative of a Permian group of termites. There is no evidence that the insect belongs to the Isoptera, but the classification in any recognized order must remain tentative at present.

GENUS *URALOTERMES* ZALESSKY

- = *Uralotermes* ZALESSKY, 1937, pp. 847, 848.
- = *Uralotermes*: ZALESSKY, 1939, pp. 53, 81.
- = *Uralotermes*: SNYDER, 1949, p. 352.
- = *Uralotermes*: EMERSON, 1955, p. 507.
- = *Uralotermes*: SHAROV, 1962, p. 133.
- = *Uralotermes*: YU AND PING, 1964, p. 19.

TYPE SPECIES: *Uralotermes permianus* Zalessky.

Uralotermes was assigned to the Isoptera by Zalessky and to the Paraplecoptera incertae sedis by Sharov.

Uralotermes permianus Zalessky

- Uralotermes permianus* ZALESSKY, 1937, pp. 847–848 (wing), fig. 3 (wing).
- Uralotermes permianus*: ZALESSKY, 1939, pp. 53, 81 (wings), fig. 30 (wings).
- Uralotermes permianus*: SNYDER, 1949, p. 352 (synonymy).
- Uralotermes permianus*: SHAROV, 1962, p. 133 (systematics), fig. 340.
- Uralotermes permianum* [sic]: McKITTRICK, 1964, p. 106 (wing).

No other species is placed in either the family or the genus. Dr. Frank Carpenter (personal communication) is preparing a manuscript in which he places the species in Insecta *incertae sedis*, because "we do not know enough of the fossil to place it in any order without considerable doubt."

The descriptions and figures are based on a wing fragment of middle Permian age from the *Sylva* basin (about latitude 57° N., longitude 56° 35' E.) in the Russian Ural Mountains. Zalessky's figures show many short superior branches of the subcosta and radius that do not conform to any known termite but are somewhat similar to the wing of *Permotermopsis* Martynov (1937, pp. 84, 445, figs. 1, 2) that Martynov assigned to the family Permotermopsidae of the order Protoblattoidea. The subcosta is comparatively very long, a character that differentiates the Protorthoptera from the Isoptera. The radius of *Permotermopsis* is much more branched than that in *Uralotermes*. The combination of a long pectinate subcosta running parallel to a pectinate radius, with only one small branch near the tip, the wide separation of the radius and media throughout most of the length of the wing except near the base where they seem to join, the extension of the media to the tip of the wing, with from five to seven inferior branches, and the extension of the cubitus to about half of the length of the wing, with two (or more) branches, provide a pattern distinct from that of any of the wings figured by Crampton (1922, pls. 5-9). It is possible, of course, that the vein homologies have been misinterpreted from the fragments of the wing.

Even without much knowledge of the Protorthoptera and without direct examination of the fragmentary type specimens, I think that *Uralotermes permianus* should be removed from the Isoptera and placed with considerable doubt in the Protorthoptera, an order of fossil insects known from the late Paleozoic and early Mesozoic eras and related to both the Orthoptera (including the Blattodea) and the Isoptera. With the removal of *Uralotermes* from the Isoptera, all known fossil species of termites are now confined to the Tertiary and Quaternary deposits, although circumstantial evidence points to the origin of the Isoptera in Paleozoic or early Mesozoic times (Emerson, 1955). Martynov (1937) is of the opinion that these orders arose from a still more primitive stock at present not known from any fossil specimens.

?ORDER

?FAMILY

GENUS *IDOMASTOTERMES* HAUPT

= *Idomastotermes* HAUPT, 1956, p. 23.

TYPE SPECIES: *Idomastotermes mysticus* Haupt.

Idomastotermes mysticus Haupt

Idomastotermes mysticus HAUPT, 1956, p. 24 (wings), fig. 16 (wings).

This genus and species are based on wings from the Eocene of Geiseltales, Germany. The latitude and longitude are not exactly known to me. I have not examined any specimen of the genus or species, and must draw my conclusions from the description and figure in Haupt (1956). The wing venation of the very fragmentary forewing and the somewhat fragmentary hind wing is unlike that of any family of termites known to me. The arrangement of veins in the costal and radial regions is labeled by Haupt as the relatively long costa and subcosta, and the radius, media, and cubitus. These run parallel to one another near the basal quarter of the wing, and the so-called subcosta shows a number of branches turning toward and joining the costal margin of the wing. The base near the humeral suture, if present, is not preserved. A portion of the anal lobe is turned under the main part of the wing and emerges beyond the costal border. Both primitive living cockroaches and the Mastotermitidae might have this character. The apical fourth of the wing, including the tip, is lacking in the specimen. The radius, as labeled, shows no short superior branches typical of the radial sector of the Mastotermitidae.

I am not convinced that the nomenclature of the veins as given by Haupt is correct, but no change in the interpretation of the homologies of the veins would make the wing conform to any known termite. I am insufficiently acquainted with the wing venation of cockroaches (see Rehn, 1951) or other orthopteroid orders to be able to assign this species to any order of insects. The Protorthoptera presumably became extinct in the early Mesozoic. If the insect is a termite, the indications are that it would have to be placed in a new family remotely related to the Mastotermitidae. In view of the fragmentary condition of the specimen, the difficulties in the recognition of the homologies of the veins, and the lack of an opportunity to examine a specimen directly, it is impossible to classify the specimen adequately. It is probably best placed in *Insecta incertae sedis* for the present.

ORDER ISOPTERA

?FAMILY

GENUS *DIATERMES* MARTYNOV

- = *Diatermes* MARTYNOV, 1929, p. 178.
- = *Diatermes*: ZEUNER, 1938, p. 116.
- = *Diatermes*: STATZ, 1939, p. 32, table 4.
- = *Diatermes*: EMERSON, 1942, p. 10.
- = *Diatermes*: SNYDER, 1949, pp. 352, 354.
- = *Diatermes*: EMERSON, 1955, p. 507.

TYPE SPECIES: *Diatermes sibiricus* Martynov.

This genus is based on the single type species and was assigned to the Mastotermitidae by Martynov. The systematic position is discussed below under the species.

Diatermes sibiricus Martynov

Diatermes sibiricus MARTYNOV, 1929, p. 179 (wing), text fig. 3 (wing), pl. 1, fig. 1 (wing).

Diatermes sibiricus: STATZ, 1939, table 4.

Diatermes sibiricus [sic]: SNYDER, 1949, p. 354.

The species is known from a portion of a wing from the upper Oligocene of Mt. Ashutas, Saisan, or Zaysan, District (latitude 47° 30' N., longitude 34° 57' E.), Siberia.

In my opinion the wing surely belongs to a termite, even though I have not been able to examine the specimen directly. In the figure and photograph the media branches from the radius about a fourth of the wing length from the base. This feature is unlike any known termite, even in the hind wing in which the media almost invariably branches from the base of the radius near the humeral suture. The media is short in or absent from a few genera of termites. What appears to be a short anal vein in *Diatermes* may indicate a hind wing, in which case the species lacks the anal lobe characteristic of the Mastotermitidae and would come closer to the Hodotermitidae, particularly the Hodotermitinae which include the fossil genus *Ulmeriella*. Zeuner (1938, p. 116) wrote that he believed *Diatermes* is related to *Ulmeriella*. In the Hodotermitinae, however, the radius has inferior inner branches that are not indicated in the figures of *Diatermes sibiricus*. The wing as a whole is even less like that of other genera of the Hodotermitidae (Emerson, 1933; Fuller, 1919). In *Diatermes* the media is closer to the radius than to the cubitus, while in the Hodotermitinae including *Ulmeriella* the media is closer to the cubitus.

The photograph of the wing seems to conform to the drawing, but further study of the specimen might reveal somewhat different connections near the base which is poorly preserved. The wing does not conform to that of any genus of the Kalotermitidae (Krishna, 1961) and cannot be placed in this family. More exacting study of the single specimen (deposition not known to me) and the collection of more material may be necessary before the species can be accurately related to other termites. I would not care to create a new family for its reception on the basis of the original description and figures of the wing fragment. I am also very doubtful whether the species is properly placed in the family Mastotermitidae where Martynov assigned it.

FAMILY MASTOTERMITIDAE DESNEUX

- < Termitidae: GOLDENBERG, 1854, p. 27.
- >< Calotermitinae FROGGATT, 1896, p. 516.
- < Calotermitinae: SILVESTRI, 1903, pp. 16, 17.
- > Mastotermitinae DESNEUX, 1904a, p. 284.
- > Mastotermitinae: DESNEUX, 1904b, p. 9.
- = Mastotermitinae: FROGGATT, 1905, p. 17.
- < Calotermitinae: HANDLIRSCH, 1906-1908, p. 697.
- = Mastotermitidae SILVESTRI, 1909, p. 280.
- = Hemiclidoptera (suborder) ENDERLEIN, 1909, p. 172.
- = Mastotermitidae: ENDERLEIN, 1909, p. 172.
- < Protermitidae HOLMGREN, 1910a, p. 285.
- = Mastotermitinae: HOLMGREN, 1910a, p. 285.
- < Protermitidae: HOLMGREN, 1910b, p. 137.
- = Mastotermitinae: HOLMGREN, 1910b, p. 137.
- = Mastotermitidae: HOLMGREN, 1911, pp. 13, 14.
- > Pliotermitinae S. PONGRÁCZ, 1917, p. 28.
- = Mastotermitidae: A. PONGRÁCZ, 1926, p. 26.
- = Mastotermitidae: TILLYARD, 1926, pp. 104, 105.
- = Mastotermitidé: BATHELLIER, 1927, p. 126.
- = Mastotermitidae: A. PONGRÁCZ, 1928, pp. 108, 113, 115.
- = Mastotermitidae: EMERSON, 1928, p. 410.
- = Mastotermitidae: KARNY, 1930, p. 432.
- = Mastotermitidae: HANDLIRSCH, 1930, pp. 843, 855, 856.
- = Mastotermitidae: BRUES AND MELANDER, 1932, pp. 93, 95.
- = Mastotermitidae: HILL, 1932, p. 9.
- = Mastotermitidae: SILVESTRI, 1934, p. 32.
- = Mastotermitidae: HARE, 1937, p. 474.
- = Mastotermitidae: MARTYNOV, 1937, pp. 86, 89, 93, 95, 96, 101-104, 107, 113, 117, 119, 123, 124, 131, 148, 149.
- < Mastotermitidae: ZEUNER, 1938, pp. 113, 115, 116.
- = Mastotermitidae: STATZ, 1939, pp. 31, 44, table 4.
- = Mastotermitidae: HILL, 1942, pp. 6, 7.
- = Mastotermitidae: EMERSON, 1942, p. 10.
- < Mastotermitidae: SNYDER, 1949, pp. 5, 9, 352.
- = Mastotermitidae: GRASSÉ, 1949, p. 529.

- = Mastotermitidae: AHMAD, 1950, p. 49.
- = Mastotermitidae: GRASSÉ, 1952, p. 70.
- = Mastotermitidae: WEIDNER, 1955, pp. 9, 36, 43, 67, 68, 74, 75.
- < Mastotermitidae: EMERSON, 1955, pp. 491, 506, 507.
- = Mastotermitidae: HARRIS, 1956, p. 435.
- < Mastotermitidae: HAUPP, 1956, p. 23.
- = Mastotermitidae: LUPOVA, 1958, p. 99.
- = Mastotermitidae: HARRIS, 1961, pp. 43, 44, 64, chart.
- = Mastotermitidae: HARRIS, 1962, pp. 193, 197.
- = Mastotermitidae: McKITTRICK, 1964, p. 52.

There has been little difference of opinion in recent years concerning the inclusion of the single living genus in the Mastotermitidae. Confusion concerning the inclusion of several genera of fossil termites has occurred among the authors. Enderlein (1909) placed the family Mastotermitidae in the suborder Hemiclidoptera of the Isoptera, but this name has not been used by other authors so far as I know and I doubt the value of making suborders for the small order Isoptera. Sándor Pongrácz (1917) made the genus *Pliotermes* the basis of the subfamily Pliotermitinae, a genus that is placed in synonymy with *Mastotermes* in this article. Zeuner (1938, p. 115) included *Ulmeriella martynovi* in the Mastotermitidae. He stated that *U. martynovi* has a hind wing with an anal lobe, but did not indicate this structure in his figures. The wings have inferior branches of the radial sector characteristic of the Hodotermitinae. The pronotum is wider in his figure 2 than in living species of the Hodotermitinae. I am leaving the species in *Ulmeriella* in the subfamily Hodotermitinae of the family Hodotermitidae until its classification can be more accurately determined.

Most authors agree that the family is, in many important respects, the most primitive family of the Isoptera and the closest to the Blattodea of the Orthoptera and to the Protorthoptera from which it probably originated (see Desneux, 1904a, 1904b; Comstock, 1918; Crampton, 1922, 1938; Browman, 1935; Ahmad, 1950, McKittrick, 1964, 1965). In some respects, the genus *Archotermopsis* of the Hodotermitidae is more primitive than the Mastotermitidae (Emerson, 1933), particularly in the dentition of the imago mandibles (Ahmad, 1950, p. 48, fig. 5). Grassé (1949, p. 531) has separated the Hodotermitidae (Emerson, 1942) into two families, the Termopsidae and the Hodotermitidae. There are no differences of opinion between Grassé and myself on the factual bases of these taxa, and the only question is the subtle and somewhat arbitrary distinction between the subfamily and family categories. I prefer not to enlarge the number of names of higher categories unless there is some major reason from the standpoint of classification and its phylogenetic and biological basis. It is true that the subfamily Hodotermitinae (= Hodotermitidae, Grassé, 1949, p. 532) has distinctive behavioral and ecological character-

istics and also has certain primitive morphological characters (i.e., a large number of antennal articles in the imago caste and relatively large pigmented eyes in the soldier caste) that indicate a radiation from an unknown primitive stock ancestral to all the living genera of the family. It is also true that *Hodotermes* and its related genera (Hodotermitinae) are close in numerous fundamental characters to the subfamily Termopsinae. *Stolotermes* is sufficiently distinct to deserve separate classification in the subfamily Stolotermitinae. Likewise *Porotermes* seems best placed in the subfamily Porotermitinae. All these subfamilies constitute the monophyletic family Hodotermitidae (see Emerson, 1942, p. 10).

I find a separation of the Isoptera into six families (Mastotermitidae, Kalotermitidae, Hodotermitidae, Rhinotermitidae, Serritermitidae, and Termitidae) adequate for the systematic and phylogenetic arrangement of all fossil and living termites sufficiently well known for a comparative study of their structural relations. The family Indotermitidae has been placed in synonymy with the subfamily Amitermitinae of the Termitidae (Krishna, 1965, p. 3), and the family Stylotermitidae Chatterjee and Thakur (1963, 1964) is insufficiently distinct from the Rhinotermitidae to deserve family status, but should be given subfamily rank as the Stylotermitinae.

Serritermes serrifer (Hagen) from Brazil is different from all other termites and is best classified in the family Serritermitidae, new family, with the monotypic subfamily Serritermitinae Holmgren (1911, pp. 62, 82) considered to be synonymous. The species has obscure phylogenetic relationships. The imago-worker mandibles (Ahmad, 1950, p. 75, fig. 17) are the most advanced of any termite genus, while the large forewing scales of the imago, and the comparatively large unpigmented eyes of the soldier, indicate a branching from an unknown stock, possibly ancestral to the Rhinotermitidae, or from primitive Rhinotermitidae. Holmgren placed the subfamily Serritermitinae in the Rhinotermitidae, while Ahmad placed it in the Termitidae. It actually does not fit into any monophyletic grouping of genera composing either family.

The Mastotermitidae include the genera *Spargotermes*, *Blattotermes*, and *Mastotermes* with little if any doubt. *Miatermes* probably belongs to the Mastotermitidae in spite of some incongruity of characters that may be due to errors of observation or interpretation. *Pliotermes* is here considered to be synonymous with *Mastotermes*. *Idomastotermes* does not belong to the Mastotermitidae and probably does not belong to the Isoptera. For the time being, *Diatermes* is left in the Isoptera in spite of considerable doubt concerning its family relationships, but the genus does not fit into the Mastotermitidae.

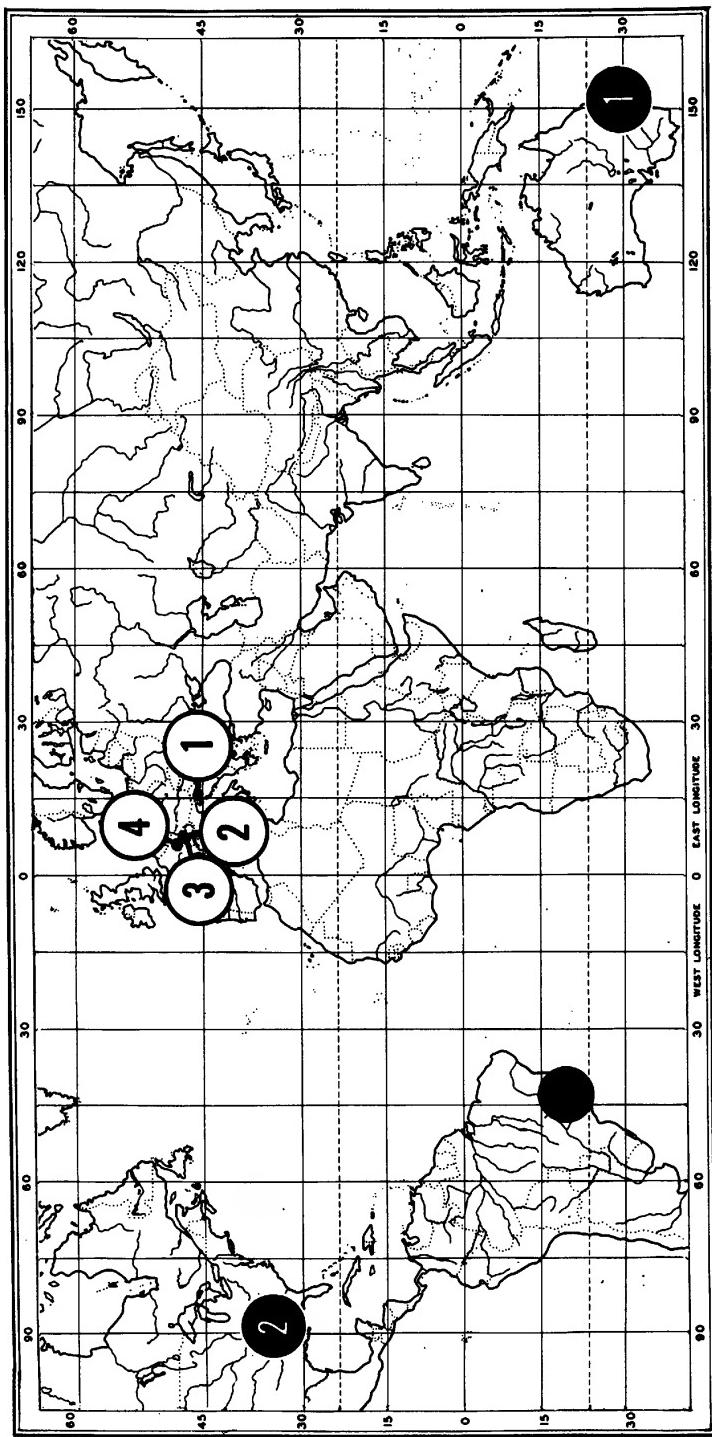


FIG. 1. Distribution of the fossil genera *Spargotermes*, *Blattopterus*, and *Miotermes*. Solid black dot: *Spargotermes costalimai*; Miocene to Pliocene of Brazil. 1 in black dot: *Blattopterus neoxenus*, Eocene (?) of Queensland. 2 in black dot: *Blattopterus wheeleri*, lower Eocene of Tennessee. 1 in white dot: *Miotermes spectabilis*, upper Miocene of Yugoslavia. 2 in white dot: *Miotermes spectabilis*, upper Miocene of Germany. 3 in white dot: *Miotermes insignis*, upper Miocene of Germany. 4 in white dot: *Miotermes randekensis*, upper Miocene of Germany.

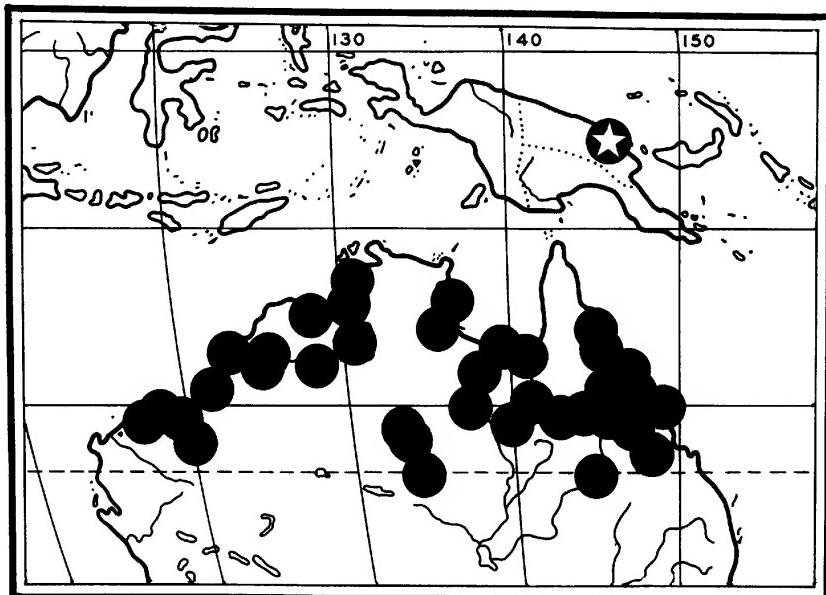


FIG. 2. Distribution of the living species, *Mastotermes darwiniensis* Froggatt. Solid dot: Known records from tropical Australia. Star in dot: Introduction by man into Lae, New Guinea.

The Tertiary distribution of the Mastotermitidae (figs. 1-3) includes every continent except Africa. This pattern is best explained by dispersion during the Mesozoic era. The time and place of origin of the family cannot be determined by means of Tertiary fossils and the present distribution of the single living species. Because of the primitive structure and wing venation of the Mastotermitidae, and the patterns of distribution of more advanced termites (Emerson, 1955), one might guess an origin in Permian or Triassic times. The northern occurrences indicate a dispersal over the northern continents to the Southern Hemisphere, rather than by an earlier southern connection through Gondwanaland in Permo-Carboniferous times (Harland and Rudwick, 1964), or by continental drift in the late Paleozoic (Darlington, 1964). However, any attempt to explain the known geographical distribution of the family must be considered highly speculative.

SPARGOTERMES, NEW GENUS

Mastotermes-like wing COSTA LIMA, 1944, p. 291, pl., 3 figs.

Mastotermitid sp. SNYDER, 1949, p. 352.

Mastotermitidae, new genus EMERSON, 1955, pp. 491, 506, 507.

TYPE SPECIES: *Spargotermes costalimai*, new species.

This new genus, based on a hind wing from Tertiary (Miocene-Pliocene) shales of Minas Gerais, Brazil (figs. 1, 4), is considered to be the most primitive genus of the Mastotermitidae. The costal border is straight for three-fourths of the length of the wing and is not thickened or rigid as in most termites. The veins starting at the humeral suture include a short subcosta, a short first radius, a short second and third radius that are joined at the base but branch into separate veins as they reach the

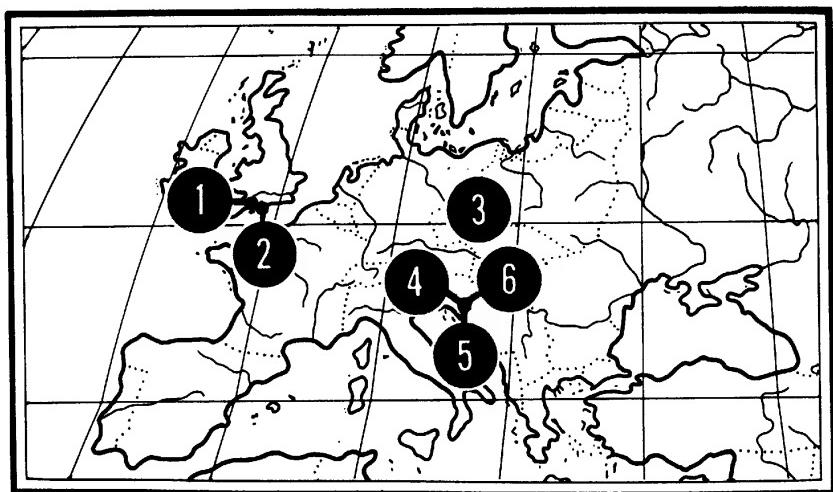


FIG. 3. Distribution of fossil species of *Mastotermes*. 1. *M. bournemouthensis*, upper Eocene of England. 2. *M. anglicus*, middle Oligocene of England. 3. *M. heerii*, upper Oligocene of Germany. 4. *M. haidingeri*, lower Miocene of Yugoslavia. 5. *M. croaticus*, lower Miocene of Yugoslavia. 6. *M. minor*, lower Miocene of Yugoslavia.

costal border, a diffuse or sprayed-out radial sector (from which character the generic name is derived), with several main superior branches that fork into more branches that reach the costal border and tip of the wing, a media that is joined for a short distance to the radial sector at the base (characteristic of the hind wing of nearly all termites) and then branches into several veins some of which extend to the tip, an anterior cubitus with several comparatively straight branches not curved inward to the degree characteristic of the large majority of termite genera, including *Blattotermes* and *Mastotermes*, of which one branch is nearly as long as the longest branch of the radial sector, a posterior cubitus that is unbranched so far as can be seen, a first anal vein with a number of short inferior branches, and a sprayed-out anal field with

four veins emerging from the basal stripe. The media in general is midway between the radial sector and the anterior cubitus but tends to be closer to the radial sector. Many branches of the anal field end before reaching the border of the large hind lobe. The veins of the anal field indicate that the anal lobe was not folded like a fan, as it is in the more advanced of the present winged cockroaches. The hind lobe is proportionately larger than that in any other genus of the Mastotermitidae and extends well over half of the length of the wing from the humeral suture. An archidictyon of irregular veinlets occurs between some of the veins and their branches in both the anal lobe and the main wing. The humeral suture is slightly curved.

The genus clearly is related to the known genera of the Mastotermitidae, particularly in the presence of the posterior cubitus and the large anal lobe of the hind wing. The diffuse, sprayed-out, radial sector and the proportionately large anal lobe indicate a more primitive condition than *Blattotermes* which has a radial sector only a little less consolidated than that of *Mastotermes* and *Miotermes*. If the genera that have been associated with the Mastotermitidae be not considered, purely for the sake of temporary convenience, *Spargotermes* shows several features of the hind wing that are the most primitive of any termite so far described and generally recognized as surely belonging to the Isoptera.

Spargotermes costalimai, new species

The species is named in honor of the late A. da Costa Lima who published a short account of the specimen (1944, pp. 291–292, plate with two photographs and one drawing) and assigned it to the Mastotermitidae without, however, naming the genus or species. His extensive studies of the Brazilian insects made him the greatest entomologist of his generation in South America. Costa Lima thought that the forewing was superimposed on top of the hind wing in the fossil, but, after considerable study, it seems that the specimen is a single hind wing (fig. 4), with the first anal vein (A_1) folded underneath and therefore appearing in reverse position, and the anal lobe severed along the anal fold, with about half of its area covered by the media-cubitus-anal portion of the main part of the wing. Some of the veins are weak or obscure, so that the description and figures are the best interpretations that I can make, but are not wholly trustworthy in all particulars. Following are the characters that are considered of specific importance without a repetition of the characters already included in the description of the genus. Some of the described characters are probably variable within the species and should be considered applicable to the individual only.

HIND WING (FIG. 4): Subcosta (Sc) unbranched, joining costal border about one-tenth of length of wing from humeral suture. First radius (R_1) unbranched, reaching costal border about one-seventh of length of wing. Second and third radius (R_2 , R_3) joined near suture and branched before reaching costal border. Radial sector (Rs) extending nearly to tip of wing, with 12 branches reaching costal border, branches sprayed out and

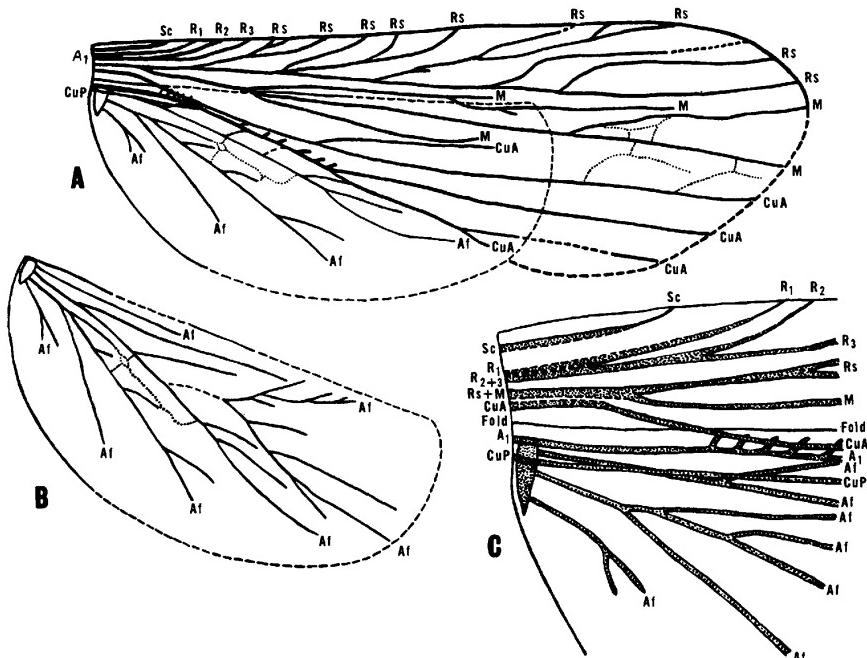


FIG. 4. Hind wing of *Spargotermes costalimai*, new genus, new species. A. Reconstruction of entire wing in preserved position, with A_1 turned under CuA , and anal lobe broken off along anal fold with half covered by M , CuA , and A_1 . B. Reconstruction of anal lobe, with veins of the anal field. C. Enlarged base of reconstructed wing in preserved position.

occupying an area about three-elevenths of width of wing. Media (M) with two branches reaching tip of wing and three or four branches seemingly terminating in membrane in outer half of wing. Anterior cubitus (CuA) with several straight branches reaching inner border of main part of wing. Anterior cubitus not separated clearly from base of radial sector and media in specimen, but was probably separated in living condition. Portion of inner branch of anterior cubitus overlapping first anal vein (A_1) which is interpreted as having been folded underneath at time of

preservation. Posterior cubitus (CuP) visible for only part of its length near humeral suture (fig. 4C). It is thought that at least part of underfolding occurred close to this vein. Because of underfolding at time of preservation, first anal vein (A_1) appearing to have a series of short superior branches, but in reality these short branches inferior, as in all well-preserved fossils of hind wings of Mastotermitidae and in living *Mastotermes*.

The full length of the posterior cubitus and first anal veins is indeterminable in the specimen, probably because they are obscured under a portion of the anterior cubitus. The anal fold is visible for part of its length and indicates by its position that the anal lobe was broken off near the posterior cubitus and first anal veins and was superimposed in part by the main portion of the wing. The anal lobe is not clearly marked at its apical border, but the veins of the anal field (not drawn in fig. 4A) cross under the anterior cubitus and media and indicate the extent and large size of the anal lobe. The veins of the anal field (Af) are more numerous and sprayed-out (fig. 4B) than in any other known species. The veinlets of the archidictyon are visible to some degree in both the main wing and in the anal lobe. It may be presumed that the archidictyon is better developed than is indicated (fig. 4A, B), but is not sufficiently well preserved to be drawn with accuracy.

MEASUREMENTS (IN MM.) OF HOLOTYPE, HIND WING: Length of preserved wing from humeral suture, 16.42; length of preserved anal lobe, 11.12; estimated length of anal lobe, 11.37; width of main part of preserved wing, 5.59; estimated width of main part of wing, 5.81; estimated width of anal lobe, 5.31.

TYPE LOCALITY AND HOLOTYPE SPECIMEN: A single hind wing preserved in brittle shale with a dip of about 30 degrees, reportedly of Miocene to Pliocene age, with leaf fragments and the elytra of a small beetle, Fonseca (latitude $20^{\circ} 10' S.$, longitude $43^{\circ} 18' W.$), on Rio Piracicaba, Municipio de Alvinopolis, Minas Gerais, Brazil (fig. 1); collected by Elias Dolianiti, No. 3904, Divisão de Geologica, Avenida Pasteur 404, Rio de Janeiro, Brazil. I am indebted to R. L. Araujo, Biologist, Departamento de Zoologia, São Paulo, Brazil, for ascertaining the exact position of the type locality. F. W. Sommer, Divisão de Geologia e Mineralogia, Rio de Janeiro, Brazil, informs me that the study of the associated plant fossils have not enabled investigators to assign the shale bed to one of the Tertiary epochs with exactitude, but it is hoped that fresh-water fish remains may provide better dating in the future.

REMARKS: It seems safe to assume that the climate was tropical at the time the species was alive. This is the fifth species of termite so far dis-

covered in what is now a tropical climate. The others are *Kalotermes* in Miocene amber from Burma, *Incisitermes* and *Heterotermes* in Miocene amber from Mexico, and *Coptotermes* in Oligocene amber from the Dominican Republic in the West Indies.

Because of the generic distinction and primitive nature of the wing venation, I am inclined to guess that this genus is the product of a Mesozoic dispersion of the Mastotermitidae around the world through the Northern Hemisphere followed by an isolation of South America from the Eocene epoch to the late Tertiary period. From the evidence at present available, we have no sound basis for guessing the exact time and place of origin of the Mastotermitidae or of any of its genera.

GENUS *BLATTOTERMES* RIEK

- < *Mastotermes*: COLLINS, 1925, pp. 406-410.
- < *Mastotermes*: SNYDER, 1949, pp. 352-354.
- < *Mastotermes*: EMERSON, 1955, p. 507.
- = *Blattotermes* RIEK, 1952, pp. 17-20.
- < *Mastotermes*: HARRIS, 1961, p. 44.

TYPE SPECIES: *Blattotermes neoxenus* Riek.

INCLUDED SPECIES: *Blattotermes wheeleri* (Collins).

Riek placed *Blattotermes* in the Mastotermitidae, but distinguished the genus from *Mastotermes* by differences in the branching of the subcosta, radius, and media. The difficulty of distinguishing such veins as the subcosta from the first radius in fossil wings makes their use questionable for generic diagnosis. I am of the opinion that *Blattotermes* is a different genus from *Mastotermes*, but not because of the characters emphasized by Riek. The more important distinctions are in the greater degree of consolidation of the radial sector and the narrower space between the successive superior branches in *Mastotermes*. *Blattotermes* is somewhat intermediate between *Spargotermes* and *Mastotermes* in this respect. So far as can be detected, it also appears that the humeral suture of the forewing is more arcuate or convex in *Mastotermes* compared to *Blattotermes*. The larger number of superior branches of the radial sector in *B. neoxenus* compared with *B. wheeleri* is possibly a species distinction. It can safely be presumed that these Eocene fossils, one from Australia and the other from North America, are distinct species. On the basis of the forewings alone, I can detect no distinction that would warrant separation of the two widely dispersed species into different genera.

Blattotermes neoxenus Riek

Blattotermes neoxenus RIEK, 1952, pp. 18-20 (forewing), fig. 1 (forewing), pl. 1, figs. 1-3 (forewing).

This species was described from a forewing from the Eocene (?) of Dinmore (about latitude 27° 34' S., longitude 152° 50' E.), Queensland, Australia (fig. 1).

Blattotermes wheeleri (Collins)

Mastotermes wheeleri COLLINS, 1925, p. 406 (forewing), fig. 2 (forewing).

Mastotermes wheeleri: STATZ, 1939, table 4.

Mastotermes wheeleri: SNYDER, 1949, p. 354.

Mastotermes wheeleri: SNYDER, 1950, p. 191.

Blattotermes wheeleri: RIEK, 1952, pp. 18-19, text fig. 2 (forewing).

Mastotermes wheeleri: HAUPT, 1956, p. 25 (forewing), fig. 17 (forewing).

This species was described from a forewing from lower Eocene deposits at Grand Junction (latitude 35° 03' N., longitude 89° 10' W.), Tennessee (fig. 1).

GENUS *MASTOTERMES* FROGGATT

< *Termes (Eutermopsis)*: GOLDENBERG, 1854, pp. 28, 29.

> *Mastotermes* FROGGATT, 1896, pp. 517, 519.

>< *Termes*: FROGGATT, 1896, p. 519.

>< *Termes*: FROGGATT, 1897b, p. 721.

= *Mastotermes*: DESNEUX, 1904a, p. 279.

> *Mastotermes*: DESNEUX, 1904b, p. 10.

>< *Termes (Termes)*: DESNEUX, 1904b, pp. 28, 35.

> *Mastotermes*: FROGGATT, 1905, p. 17.

>< *Termes*: FROGGATT, 1905, p. 26.

= *Mastotermes*: SILVESTRI, 1909, p. 284.

= *Mastotermes*: HOLMGREN, 1910a, p. 285.

= *Mastotermes*: HOLMGREN, 1911, p. 15.

= *Mastotermes*: BUGNION, 1914, p. 174.

> *Mastotermes*: S. PONGRÁCZ, 1917, p. 33.

> *Pliotermes* S. PONGRÁCZ, 1917, p. 28.

< *Mastotermes*: COLLINS, 1925, pp. 406-410.

= *Mastotermes*: SNYDER, 1925, p. 155.

= *Mastotermes*: HILL, 1925, pp. 119-124.

= *Mastotermes*: EMERSON, 1926, p. 92.

> *Mastotermes*: A. PONGRÁCZ, 1926, p. 25.

> *Pliotermes*: A. PONGRÁCZ, 1926, p. 26.

= *Mastotermes*: TILLYARD, 1926, pp. 102, 105.

= *Mastotermes*: EMERSON, 1928, p. 405.

> *Mastotermes*: A. PONGRÁCZ, 1928, pp. 102-108.

> *Pliotermes*: A. PONGRÁCZ, 1928, pp. 107, 112.

= *Mastotermes*: HANDLIRSCH, 1930, p. 855.

> *Pliotermes*: A. PONGRÁCZ, 1931, p. 106.

= *Mastotermes*: TILLYARD, 1931, pp. 371-390.

= *Mastotermes*: SILVESTRI, 1934, pp. 28, 32.

= *Mastotermes*: HARE, 1937, p. 474.

- = *Mastotermes*: MARTYNOV, 1937, pp. 87–150.
> *Mastotermes*: ZEUNER, 1938, pp. 115, 116.
> *Pliotermes*: ZEUNER, 1938, p. 115.
> *Pliotermes*: STATZ, 1939, p. 32, table 4.
> *Mastotermes*: EMERSON, 1942, pp. 7–10.
> *Pliotermes*: EMERSON, 1942, p. 10.
= *Mastotermes*: HILL, 1942, pp. 7, 11, 14, 15.
>< *Mastotermes*: SNYDER, 1949, p. 352.
> *Pliotermes*: SNYDER, 1949, pp. 352, 354.
= *Mastotermes*: WEIDNER, 1955, pp. 31, 44.
>< *Mastotermes*: EMERSON, 1955, pp. 476, 498, 507.
> *Pliotermes*: EMERSON, 1955, p. 507.
= *Mastotermes*: NOIROT AND KOVOOR, 1958, p. 439.
= *Mastotermes*: CALABY AND GAY, 1959, pp. 211, 212, 215.
< *Mastotermes*: HARRIS, 1961, p. 44.
= *Mastotermes*: HARRIS, 1962, pp. 193, 196, 197, 200, 201.
= *Mastotermes*: MARKS AND LAWSON, 1962, pp. 139–143, 145, 156, 157.
= *Mastotermes*: McKITTRICK, 1964, pp. 52, 53, 74, 75, 98–102, 106, 107, 111, pl. 5, figs. 11–13, pl. 50, figs. 135–137.

TYPE SPECIES: *Mastotermes darwiniensis* Froggatt.

INCLUDED SPECIES: *Mastotermes bournemouthensis* Rosen, *M. anglicus* Rosen, *M. heerii* (Goeppert), *M. haidingeri* (Heer), *M. croaticus* Rosen, *M. minor* A. Pongrácz.

The genus was described by Froggatt (1896) for the living species *M. darwiniensis* from tropical Australia. The soldier of *M. darwiniensis* was first described under the name *Termes errabundus* Froggatt (1897b, p. 733), but was soon recognized as conspecific with the earlier described imago. The primitive morphology of *M. darwiniensis* has resulted in a voluminous literature dealing with both the genus and species, most of which will be found in the appended bibliography. There is general agreement that a great many features of the anatomy indicate that *M. darwiniensis* is a very primitive relict type, particularly in the structure of the thorax, including the wings and legs, and in the structure of the reproductive organs and appendages in the abdomen (McKittrick, 1964, 1965). The discovery that the eggs are laid in an oothecal mass helps to substantiate the relations of *Mastotermes* to the Orthoptera, particularly to the cockroaches. However, *Mastotermes* is not the most primitive living termite in certain important respects (Emerson, 1933, 1942). In particular, the imago mandibles, cerci, and styli of *Archotermopsis* are more primitive, thus indicating that an undiscovered generalized termite ancestral to the Mastotermitidae and Hodotermitidae must have preceded the origin of these two families in late Paleozoic or early Mesozoic ages. The social behavior and organization of *Archotermopsis* (Imms, 1919) in many respects are also more primitive than those among the living *Mastotermes*.

The living *Mastotermes darwiniensis* is confined approximately to the tropical portion of Australia north of the Tropic of Capricorn (fig. 2). Calaby and Gay (1959, pp. 211, 215, 222) noted the distribution in both coastal and inland areas which vary considerably in the amounts of rainfall and soil moisture, but also stated that the species is absent from rain-forest soils and soils that once carried rain forest (see Ratcliffe, Gay, and Greaves, 1952, p. 33). During the Second World War *M. darwiniensis* was introduced into Lae, New Guinea, where it was still flourishing in 1963 in spite of the strenuous measures by government entomologists to eradicate it. Lae is surrounded by rain forests at sea level, and rain forests surely covered the area before the advent of man, so we must conclude that fairly wet soils are not a limiting factor for the species, although it is confined to buildings, posts, logs, and soils in Lae that are in cleared areas modified by modern man. In common with nearly every case of introduction of a termite species, *M. darwiniensis* has not invaded the surrounding natural forests or swamps that have a rich native termite fauna. The established native termites may provide a biotic barrier to the dispersal of *M. darwiniensis* beyond the man-modified habitats (see Allee *et al.*, 1949, p. 723). The existence or lack of biotic barriers is highly important for any program of economic control. In Australia, *M. darwiniensis* often attacks living trees, shrubs, and sugarcane that is not grown in rain forest soils.

To what extent the ecological distribution of the single relict species of *Mastotermes* may provide a clue to the ecological requirements of the fossil species is a question. The fossil species (fig. 3) have been found in several localities that are now temperate, but all of these localities might have been tropical during the various Tertiary periods (Chandler, 1964). Cockerell (1915, p. 481) suggested that the Oligocene of Gurnet Bay, Isle of Wight, England, which contains fossils of *M. anglicus*, gives indications of a fauna that lived in a more temperate climate than that of Baltic amber of an earlier period. No specimen of the genus *Mastotermes* or the family Mastotermitidae has been found in Baltic amber, which clearly exhibits a warm temperate fauna and flora, but the absence of a fossil obviously does not mean that a mastotermitid did not occur near the Baltic Sea. The termite fauna of the Florissant shales in Colorado is also typical of a temperate climate, and again the Mastotermitidae are absent so far as is known.

It is possible that the Mastotermitidae were wholly tropical in their distribution, but it is also possible but not proved that some species invaded warm temperate climates during the climatic shifts of the last 63 million years. The genus *Reticulitermes* (Rhinotermitidae) is essentially an

indicator of a temperate climate, although it overlaps slightly a tropical fauna on its extreme southern border. Species of *Reticulitermes* are known from Baltic amber (upper Eocene or lower Oligocene), Florissant shales, Colorado (upper Oligocene or lower Miocene), and from Radoboj, Croatia, Yugoslavia (upper Miocene). The species from Radoboj is *Reticulitermes hartungi* (Heer), new combination, formerly placed in *Termitidae*, *Leucotermes*, and *Heterotermes* (Emerson, MS in preparation). The Radoboj shales also contain *Mastotermes haidingeri* (Heer), *M. croaticus* Rosen, *M. minor* A. Ponrácz, and *Miotermes procerus* (Heer).

That a single species of *Mastotermes* survives and flourishes in tropical Australia in competition with a large fauna of advanced tropical termites is rather astonishing, and the extinction of the family elsewhere in the world by the end of the Tertiary period has no ready explanation.

We do not know the time or place of the origin of *Mastotermes*, but the distribution of the fossil species (fig. 3) indicates that the genus was widespread by early Tertiary times and did not necessarily originate in Australia.

Mastotermes darwiniensis Froggatt

In this review, which emphasizes the fossil species, I think it inappropriate to repeat the information and voluminous references to the living species from tropical Australia (fig. 2). I have 49 bibliographical citations to the species, most of which are contained in the appended bibliography and the references to the genus *Mastotermes* and the family Mastotermitidae. Hill (1942, p. 15) and Snyder (1949, p. 10) have listed some of these references. Others will be found in the discussions of the family, genera, and species in this article.

A fascinating aspect of the biology of *Mastotermes darwiniensis* is the associated symbiotic organisms in the hind gut. Cleveland and Grimstone (1964) discussed the polymastigote flagellate, *Mixotricha paradoxa* Sutherland, belonging to the order Trichomonadina and related to the Devescovinidae. This protozoan has three or four kinds of microorganisms living in or on it, the cell surface is remarkably adapted to accommodate spirochaetes and bacteria, and some (spirochaetes) function as a locomotor apparatus for the flagellate. The cytoplasm of *Mixotricha* is filled with wood that is probably digested by the protozoan and provides the nutrients for the termites and their associated organisms. The function of the bacteria is unknown. Seevers (1957, pp. 58, 280) records a physogastric termiteophilous staphylinid beetle, *Mastopsenius australis* Seevers, from colonies of *Mastotermes darwiniensis*, and assigns the beetle to the subfamily Trichopseniinae, most of the genera of which are found with

various host termites of the family Rhinotermitidae. It is obvious that *Mastotermes darwiniensis* is the focal species at the center of a biocoenose composed of the termite, numerous species of protozoans, spirochaetes, bacteria, and a beetle, all of which indicate a phylogeny of an ecosystem involving mutual adaptation, cooperation, and interdependence, which must have originated with the cockroach-like ancestors of the termites.

Mastotermes bournemouthensis Rosen

Mastotermes bournemouthensis ROSEN, 1913, p. 320 (wings), pl. 26, figs. 3, 4 (forewing, hind wing).

Mastotermes bournemouthensis: COCKERELL, 1915, p. 471.

Mastotermes bournemouthensis: SNYDER, 1925, chart.

Mastotermes bournemouthensis: COLLINS, 1925, p. 409 (forewing), fig. 4 (forewing).

Mastotermes bournemouthensis: A. PONGRÁCZ, 1926, pl. 3, fig. b (wing), pl. 5 (phylogenetic tree).

Mastotermes bournemouthensis: A. PONGRÁCZ, 1928, p. 108.

Mastotermes bournemouthensis: A. PONGRÁCZ, 1931, p. 106.

Mastotermes bournemouthensis: STATZ, 1939, table 4.

Mastotermes(?) bournemouthensis: SNYDER, 1949, p. 353.

Mastotermes bournemouthensis: HAUPT, 1956, p. 25, fig. 18 (wing).

Mastotermes bournemouthensis: HARRIS, 1961, p. 44.

This species was described from wing fragments from the upper Eocene Bagshot beds of Bournemouth (latitude 50° 43' N., longitude 1° 54' W.), Hampshire, England (fig. 3), which are deposited in the British Museum (Natural History).

The wings are not complete enough for one to be positive that the species belongs to *Mastotermes*, but all visible characters of both forewing and hind wing conform to the generic characters. The shape of the humeral suture is not known. The published drawings of the wings do not show clear specific distinctions from the other species of the genus. The more convexly curved radial sector is different from the straighter radial sector of *M. darwiniensis* and *M. anglicus*.

Mastotermes anglicus Rosen, new synonymy

Mastotermes anglicus ROSEN, 1913, pp. 321, 322 (forewing and hind wing), pl. 27, figs. 5-8 (forewing, hind wing).

Mastotermes Batheri ROSEN, 1913, pp. 321, 322 (hind wing), pl. 28, fig. 9 (hind wing).

Mastotermes anglicus: COCKERELL, 1915, p. 471.

Mastotermes Batheri: COCKERELL, 1915, p. 471.

Mastotermes anglicus: SNYDER, 1925, chart.

Mastotermes batheri: SNYDER, 1925, chart.

Mastotermes anglicus: COLLINS, 1925, p. 409 (forewing), fig. 7 (forewing).

Mastotermes batheri: COLLINS, 1925, p. 409 (hind wing), fig. 6 (hind wing).

Mastotermes anglicus: A. PONGRÁCZ, 1928, pp. 108, 112.

- Mastotermes batheri*: A. PONGRÁCZ, 1928, p. 108.
Mastotermes anglicus: A. PONGRÁCZ, 1931, p. 106.
Mastotermes anglicus: MARTYNOW, 1937, pp. 90, 95, 124.
Mastotermes anglicus: STATZ, 1939, table 4.
Mastotermes batheri: STATZ, 1939, table 4.
Mastotermes anglicus: SNYDER, 1949, p. 352.
Mastotermes batheri: SNYDER, 1949, p. 353.
Mastotermes anglicus: HAUPP, 1956, p. 25, fig. 20 (forewing).
Mastotermes batheri: HAUPP, 1956, p. 25, fig. 19 (hind wing).
Mastotermes anglicus: HARRIS, 1961, p. 44.
Mastotermes batheri: HARRIS, 1961, p. 44.

This species was described from the wings and bodies of three specimens from Bembridge limestone, middle Oligocene, of Gurnard, or Gurnet, Bay, Bembridge (latitude 50° 41' N., longitude 1° 05' W.), Isle of Wight, England (fig. 3). A fragment of a hind wing from the same stratum and locality was described under the name of *Mastotermes Batheri* by Rosen. I have examined the holotype of *M. batheri* in the British Museum (Natural History) and compared it with the holotype and paratypes of *M. anglicus* and find no differences that seem sufficient to warrant the separation of these species. I am therefore placing *M. batheri* in synonymy with *M. anglicus*. *Mastotermes anglicus* seems to have a greater proportional distance between the costal border and the radial sector than does *M. darwiniensis*.

Mastotermes heerii (Goeppert)

- Termopsis Heerii* GOEPPERT, 1855, p. vii (wing).
Termopsis Heeriana GOEPPERT, 1855, pl. 26, fig. 53 (wing).
Hodotermes Heerianus: ASSMANN, 1870, p. 45, pl. 1, fig. 7 (wing).
(*Termopsis*) *Heeri*: HANDLIRSCH, 1906-1908, p. 699.
Mastotermes heeri: SNYDER, 1925, chart.
Mastotermes heerianus: SNYDER, 1925, chart.
Mastotermes heerii: EMERSON, 1933, p. 191 (wing).
Termopsis heeri: STATZ, 1939, table 4.
Mastotermes heeri: SNYDER, 1949, p. 353.

Goeppert described and figured the outer portion of a wing which he first named *Termopsis Heerii* and later changed to *Termopsis Heeriana*. The fossil was found in upper Oligocene deposits in Schossnitz (latitude 51° 02' N., longitude 16° 48' E.), Schlesien, Germany (fig. 3).

The radial sector has only four superior branches in the preserved apical portion, the media has four branches that reach close to the tip of the wing, and the media is closer to the radial sector than to the anterior cubitus in the outer portion of the wing. The anterior cubitus reaches near the tip with many branches. An archidictyon of irregular veinlets occurs between the true veins. The tips of veins that may be the posterior

cubitus and the first anal are figured, suggesting that the fragment is probably the apical portion of a hind wing. The compact radial sector and the fact that the media is closer to the radial sector than to the anterior cubitus indicate that the species belongs to *Mastotermes*. Distinction from other species in the genus is not clear, but the location and stratum make it unlikely that *M. heerii* is the same as any other described species.

Mastotermes haidingeri (Heer), new synonymy

Termes (Termopsis) Haidingeri HEER, 1849a, p. 26 (imago).

Termes Haidingeri: HEER, 1849b, p. 87.

Termes (Eutermopsis) Haidingeri: GOLDENBERG, 1854, p. 28, pl. 5, fig. 1 (wing).

Termopsis Haidingeri: GIEBEL, 1856, p. 293 (wing).

Hodotermes Haidingeri: HAGEN, 1858a, pp. 98, 459 (imago).

Hodotermes Haidingeri: HAGEN, 1858b, p. 15 (imago).

(*Termopsis*) *Haidingeri*: HANDLIRSCH, 1906-1908, p. 698.

"*Termes Haidingeri*": ROSEN, 1913, p. 323.

Miotermes haidingeri: SNYDER, 1925, chart.

Mastotermes Haidingeri: A. PONGRÁCZ, 1928, pp. 102, 108, text figs. 2, 3 (wings).

Mastotermes vetustus A. PONGRÁCZ, 1928, pp. 106-108 (forewing, hind wing), fig. 5 (forewing, hind wing).

Mastotermes haidingeri: EMERSON, 1933, p. 191.

Mastotermes haidingeri: STATZ, 1939, table 4.

Mastotermes vetustus: STATZ, 1939, table 4.

Mastotermes haidingeri: SNYDER, 1949, p. 353.

Mastotermes vetustus: SNYDER, 1949, p. 354.

The fossil imago was described from the lower Miocene of Radoboj (latitude 46° 06' N., longitude 15° 59' E.), Croatia, Yugoslavia (fig. 3). Several species of *Mastotermes* and *Miotermes* have been named from fossil specimens from the same deposits and locality. It seems unlikely that so many related species of termites should occur together, and I suspect that several may ultimately prove to be synonyms. However, I am placing one only, *Mastotermes vetustus* Pongrácz, in synonymy with *M. haidingeri*. Alexander Pongrácz distinguished these species primarily by the separation of the radial sector from the base of the media in the hind wing, and also by the difference in the branching of the media. In my opinion, the radial sector and media are always joined at the base just beyond the humeral suture in the hind wing of the Mastotermitidae and in most other termites. Fossil wings often have the base broken or folded, making the distinction of the veins near the humeral suture difficult to see or to reconstruct. I therefore think the specific distinctions given by A. Pongrácz are invalid. The size of the wings is close in the specimens.

The descriptions and figures of *M. haidingeri* indicate that there is confusion and possible error in the interpretations of the venation. The fig-

ures of the hind wing in A. Ponrácz (1928, figs. 2, 5) seem to fit the pattern of *Mastotermes*, although the branches of the media are somewhat unusual. Inferior branches of the radial sector are also not typical of *Mastotermes*. The branches of the radial sector are interpreted as superior in the figure by Goldenberg (1854, pl. 5, fig. 1). These characters may possibly be specific but are more likely to be variations that often occur in termites of the same species. The anal lobe of the hind wing is characteristic of *Mastotermes* and related genera.

Mastotermes croaticus Rosen, new synonymy

Mastotermes croaticus ROSEN, 1913, p. 324 (hind wing), pl. 28, fig. 10 (hind wing).

Pliotermes hungaricus S. PONGRÁCZ, 1917, p. 28 (hind wing), figs. 1, 2 (hind wing).

Mastotermes croaticus: SNYDER, 1925, chart.

Mastotermes croaticus: COLLINS, 1925, p. 409 (hind wing), fig. 5 (hind wing).

Mastotermes croaticus: A. PONGRÁCZ, 1926, p. 26, pl. 3c (hind wing), pl. 5 (phylogenetic tree).

Pliotermes hungaricus: A. PONGRÁCZ, 1926, pp. 26, 27 (hind wing), pl. 3a (hind wing), pl. 5 (phylogenetic tree).

Mastotermes croaticus: A. PONGRÁCZ, 1928, pp. 101, 102, 108, 112, 113 (hind wing).

Pliotermes hungaricus: A. PONGRÁCZ, 1928, pp. 107, 108, 113 (hind wing).

Mastotermes croaticus: HANDLIRSCH, 1930, fig. 905 (hind wing).

Mastotermes croaticus: A. PONGRÁCZ, 1931, p. 106.

Pliotermes hungaricus: A. PONGRÁCZ, 1931, p. 106.

Mastotermes croaticus: STATZ, 1939, table 4.

Pliotermes hungaricus: STATZ, 1939, table 4.

Mastotermes croaticus: SNYDER, 1949, p. 353.

Pliotermes hungaricus: SNYDER, 1949, p. 354.

Mastotermes croaticus: HAUPP, 1956, p. 25, fig. 21 (hind wing).

The species is based on a hind wing from Radoboj, Yugoslavia, in the same horizon and locality as *M. haidingeri* (fig. 3). I cannot detect either generic or specific differences in *Pliotermes hungaricus* S. Ponrácz and am placing this name in synonymy with *Mastotermes croaticus*.

The veins near the tip are more convex than these in *M. anglicus*, *M. bournemouhensis*, and *M. darwiniensis*. The anal field as figured by A. Ponrácz (1926, pl. 3c) is probably incorrect, as I know of no species of the Mastotermitidae that has a single vein in the anal lobe with a series of inferior branches. The reconstructed vein may have been suggested by the first anal which, however, should have short inferior branches as it does in the original figures by Rosen and S. Ponrácz.

The described differences in the branching of the subcosta, the number of superior veins in the radial sector, the branching of the media, and the basal inferior branches of the anterior cubitus are here considered either to be within the normal variation of the species, errors of observa-

tion, or defects in the preservation of the specimens. I am also of the opinion that *M. croaticus* possibly may be a synonym of *M. haidingeri*. *Mastotermes croaticus*, however, appears to have more convex veins near the tip of the wing than do *M. haidingeri* and other species of *Mastotermes*. Without the opportunity to examine the specimens at first hand, I think it best to leave *M. croaticus* separated for the time being. It is also possible that *Miotermes procerus* (Heer) from the same stratum and locality is synonymous. If this suggestion is shown to be correct, *Miotermes* would become a synonym of *Mastotermes*, and the species name *procerus* has page priority over *haidingeri* in Heer (1949a).

Mastotermes minor A. Pongrácz

Mastotermes minor A. PONGRÁCZ, 1928, pp. 105, 108 (hind wing), figs. 2, 4 (hind wing).

Mastotermes minor: STATZ, 1939, table 4.

Mastotermes minor: SNYDER, 1949, p. 354.

This species was described from a hind wing from the lower Miocene of Radoboj in the same stratum and locality as *M. haidingeri*, *M. croaticus*, and *Miotermes procerus* (fig. 3). The major difference from the other species of Mastotermitidae in the same deposits is the size of the hind wing. The length of the hind wing is 18 mm., and the width is 9 mm., in contrast to that of *M. haidingeri* with a length of 30.5 mm. and a width of 10.1 mm. The strongly convex radial sector and media near the tip resemble those of *M. croaticus* in which, however, the length of the hind wing is 29 mm. I question the interpretation of the long costa in A. Pongrácz's description and figure, and think this vein must be a part of the radial complex if the species belongs to the Isoptera. If the vein is the first, second, or third radius, however, it is remarkably long in contrast to that of other species of the Mastotermitidae.

GENUS MIOTERMES ROSEN

- < *Termes (Termopsis)* HEER, 1849a, p. 23.
- < *Hodotermes*: HAGEN, 1858a, p. 81.
- < *Hodotermes (Hodotermes)*: HAGEN, 1858b, p. 13.
- < *Miotermes* ROSEN, 1913, p. 325.
- < *Termopsis*: COCKERELL, 1916, p. 138.
- < *Termopsis*: BANKS AND SNYDER, 1920, pp. 8, 9, 11, 77.
- < *Termopsis*: SNYDER, 1925, p. 157.
- = *Miotermes*: A. PONGRÁCZ, 1926, p. 25.
- = *Miotermes*: A. PONGRÁCZ, 1928, p. 101.
- = *Miotermes*: STATZ, 1939, p. 32, table 4.
- = *Miotermes*: EMERSON, 1942, p. 10.
- = *Miotermes*: SNYDER, 1949, p. 355.

= *Miotermes*: EMERSON, 1955, p. 507.

TYPE SPECIES: *Miotermes procerus* (Heer).

INCLUDED SPECIES: *Miotermes randeckensis* Rosen, *M. spectabilis* (Heer), and *M. insignis* (Heer).

The various described characters of generic importance do not seem to make a consistent pattern which might be expected in a separate genus of Mastotermitidae, and I am inclined to infer that some of them are errors of observation, interpretation, or due to poor preservation that can be corrected only through direct study of types and other specimens.

Miotermes was described by Rosen (1913) with a mandibular dentition like that of *Hodotermes*, and his figure (pl. 29, fig. 14) does resemble the *Hodotermes* left mandible more than that of *Mastotermes* (see Ahmad, 1950, figs. 5, 6). The left mandible of *Mastotermes* shows the complete fusion of the first and second marginal teeth, in this respect resembling the left mandible of the Kalotermitidae, while in the Hodotermitidae there is a graded series of genera showing stages in the fusion of the first and second marginal teeth which, however, never fuse to the extent that the point of the second marginal tooth is obliterated. In view of the known consistency of the dentition, it is difficult to conceive that a *Hodotermes*-like mandible could be associated with other characteristics that clearly fit the family Mastotermitidae, and I am not convinced that the description and drawing by Rosen are correct.

The shape of the head of *Miotermes* (= "Termites") *procerus* (Heer, 1849a, pl. 2, figs. 5, 5b) is surely incorrect. No termite has the illustrated bilobed hind margin of the head. The wide pronotum figured by Heer (1849a) and Rosen (1913, pl. 29, fig. 14) is not like that of any genus of Hodotermitidae (except possibly *Ulmeriella* in which the proportional width of the pronotum to the width of the head is not clearly established) and does resemble that of *Mastotermes darwiniensis*. The presence of ocelli in the Mastotermitidae and their absence from the Hodotermitidae are important distinguishing characters separating these two families, but whether the lack of mention of the ocelli in the description or their absence from the figure means that they were not present in the living termite before fossilization cannot be determined without more well-preserved fossils or re-examination of those scattered type specimens that were not destroyed during the Second World War.

On the basis of the figured wings and descriptions by Rosen (1913) and A. Pongrácz (1926), I am inclined to place *Miotermes* in the Mastotermitidae for the present. The hind wing figured by A. Pongrácz has an anal lobe that resembles that of *Mastotermes*. The hind wing has a larger area occupied by the media and a smaller area occupied by the anterior

cubitus than in *Mastotermes* or *Blattotermes neoxenus*, but resembles *B. wheeleri* in this respect. The generic stability of this character is not known, although the various living and fossil species of *Mastotermes* indicate a fair degree of consistency. The humeral suture of the forewing of *Miotermes procerus* (Rosen, 1913, pl. 28, fig. 11) is not so strongly curved as in *Mastotermes*, but resembles that of *Blattotermes wheeleri* and is a little more convex than that of *B. neoxenus*. If the humeral suture is adequately preserved and correctly drawn, this character combined with the wings is sufficiently different from that in *Mastotermes*, *Blattotermes*, and *Spargotermes* to provide grounds for separate generic status of *Miotermes* within the family Mastotermitidae. The greater curve of the humeral suture is considered to be a derivative character (Emerson, 1962).

The generic and family characters in the descriptions and figures of *Miotermes procerus* (Heer) are (1) the less convex curve of the humeral suture of the forewing compared with that of *Mastotermes darwiniensis* and *M. anglicus*; (2) the proximity of the media to the radial sector rather than to the cubitus in both wings; (3) the compact radial sector compared with that of *Spargotermes* and *Blattotermes*; (4) the dentition of the mandibles as reported by Rosen which, if correct, would be sufficient to remove *Miotermes* from the Mastotermitidae; (5) the wide pronotum in relation to the head width which is in agreement with *Mastotermes* and not in agreement with any living genus of the Hodotermitidae; (6) the absence of ocelli, in agreement with the Hodotermitidae but not with the Mastotermitidae; (7) the well-developed archidictyon, in agreement with the Mastotermitidae and Hodotermitidae, but not characteristic of the Kalotermitidae, Rhinotermitidae, or Termitidae; (8) the anal lobe of the hind wing in the reconstruction by A. Pongrácz (1926, pl. 4, fig. d), in agreement with the Mastotermitidae; and (9) the short anterior cubitus in the reconstruction of the hind wing (A. Pongrácz, 1926, pl. 4, fig. d) compared with the other genera and species of the Mastotermitidae. The factual basis of the reconstruction of the hind wing by A. Pongrácz is not known.

It can be seen from the list of described characters that their association is not consistent with any of the recognized families of termites, but it is also apparent that those characters not in conformity with the concept of the family Mastotermitidae are based on inadequately preserved or questionably interpreted specimens. The unquestioned characters of *Miotermes* are close to the genus *Mastotermes*, and possibly further study will show that these two genera are synonymous. In view of the information available to me, it seems best for the present to treat *Miotermes* tentatively as a separate genus of the Mastotermitidae, with the hope that

additional study of both known and new specimens will enable us to correct errors in the literature and establish the true relations of *Miotermes*.

Miotermes procerus (Heer)

- Termes pristinus* CHARPENTIER, 1843, pl. 23, fig. 4 (imago) [only].
Termes (Termopsis) procerus HEER, 1849a, p. 23 (imago), pl. 2, fig. 5 (imago).
Termes (Termopsis) procerus: GIEBEL, 1852, p. 638.
Termes (Termopsis) procerus: GIEBEL, 1856, p. 292.
Hodotermes procerus: HAGEN, 1858a, p. 97 (imago).
Hodotermes procerus: HAGEN, 1858b, p. 15 (imago).
Termopsis procerus: HANDLIRSCH, 1906–1908, p. 698.
Miotermes procerus: ROSEN, 1913, pp. 323–325 (imago), pl. 28, fig. 11 (wings), pl. 29, fig. 14 (head, pronotum).
Termopsis procerus: COCKERELL, 1916, p. 138 (wings).
Miotermes procerus: SNYDER, 1925, chart.
Miotermes procerus: A. PONGRÁCZ, 1926, pl. 4d (hind wing), pl. 5 (phylogenetic tree).
Miotermes procerus: A. PONGRÁCZ, 1928, pp. 101, 102, 108.
Miotermes procerus: A. PONGRÁCZ, 1931, p. 106.
Miotermes procerus: EMERSON, 1933, p. 191.
Miotermes procerus: STATZ, 1939, table 4.
Miotermes procerus: SNYDER, 1949, p. 355.

The characters discussed under the genus *Miotermes* are based largely on this species from the lower Miocene of Radoboj (latitude 46° 06' N., longitude 15° 59' E.), Croatia, Yugoslavia (fig. 1). Handlirsch (1906–1908, p. 24) stated that the figure labeled "*Termes pristinus*" in Charpentier (1843, pl. 23, fig. 4) should be referred to *Miotermes* (= "*Termes*") *procerus* and not to *Termes pristinus* (tentatively assigned to *Macrotermes* at the present time). The figure is too lacking in detail for me to make any critical comment on this synonymy.

Miotermes randeckensis Rosen

- Miotermes randeckensis* ROSEN, 1913, p. 326 (imago).
Miotermes randeckensis: SNYDER, 1925, chart.
Miotermes randeckensis: A. PONGRÁCZ, 1926, pl. 5 (phylogenetic tree).
Miotermes randeckensis: STATZ, 1939, table 4.
Miotermes randeckensis: SNYDER, 1949, p. 355 (several references incorrect).

This species was described from a forewing from the upper Miocene of Randeck (not exactly located), Württemburg, Germany (fig. 1). The center of Württemburg is about latitude 48° 35' N., longitude 9° 22' E. The type specimen is reported to be in Stuttgart Naturalienkabinett. No figure of the wing has been published. The description of the wing indicates that it is closer in size to that of *M. procerus* than to that of *M. spectabilis*. Otherwise the species is close to *M. procerus* in its pronotum. No

specific characters of much significance are recorded, but the geological horizon and locality preclude placing the species in synonymy without more evidence. Until further studies are made, the status of the species must remain in doubt.

Miotermes spectabilis (Heer)

- Termes (Termopsis) spectabilis* HEER, 1849a, p. 28 (imago), pl. 2, fig. 6 (imago).
Termes (Termopsis) spectabilis: GIEBEL, 1852, p. 638.
Termes (Termopsis) spectabilis: GIEBEL, 1856, p. 293.
Hodotermes spectabilis: HAGEN, 1858a, p. 99 (imago).
Hodotermes spectabilis: HAGEN, 1858b, p. 15 (imago).
(Termopsis) spectabilis: HANDLIRSCH, 1906-1908, p. 698.
Miotermes spectabilis: ROSEN, 1913, pp. 324, 325, 326.
Miotermes spectabilis: SNYDER, 1925, chart.
Miotermes spectabilis: EMERSON, 1933, p. 191.
Miotermes spectabilis: STATZ, 1939, table 4.
Miotermes spectabilis: SNYDER, 1949, p. 355.

The species is known from a fossil imago with head, pronotum, and overlapping wings in the collection in Stuttgart originally found in upper Miocene deposits of Oeningen, or Öhningen (latitude 47° 39' N., longitude 8° 53' E.), Baden, Germany (fig. 1). The size (length of wings, 41.0 mm.) is close to that of *M. procerus* (length with wings, 42.0 mm.). *Miotermes insignis*, from the same horizon and locality, is smaller (length with wings, 35.0 mm.). I cannot determine the significance of this difference in size and have no new data that would justify a change in the present status of the species. The length of the whole insect with wings is difficult to measure accurately even in a series of living imagoes, and in many species the females are larger than the males.

Miotermes insignis (Heer)

- Termes (Termopsis) insignis* HEER, 1849a, p. 29 (imago), pl. 3, fig. 1 (imago).
Termes (Termopsis) insignis: GIEBEL, 1852, p. 638.
Termes (Termopsis) insignis: GIEBEL, 1856, p. 293.
Hodotermes insignis: HAGEN, 1858a, p. 100 (imago).
Hodotermes insignis: HAGEN, 1858b, p. 15 (imago).
(Termopsis) insignis: HANDLIRSCH, 1906-1908, p. 698.
Miotermes insignis: ROSEN, 1913, pp. 324-326.
Termopsis insignis: BANKS AND SNYDER, 1920, p. 9.
Miotermes insignis: SNYDER, 1925, chart.
Miotermes insignis: EMERSON, 1933, p. 191.
Miotermes insignis: STATZ, 1939, table 4.
Miotermes insignis: SNYDER, 1949, p. 355.

This species was described and figured from an entire insect from the

upper Miocene of Oeningen, or Öhningen (latitude $47^{\circ} 39'$ N., longitude $8^{\circ} 53'$ E.), Baden, Germany (fig. 1), from the same horizon and locality as *M. spectabilis*. Banks (Banks and Snyder, 1920, p. 9) erroneously made it the type species of *Termopsis* (see Emerson, 1933, pp. 165, 166), and it was assigned to *Miotermes* by Rosen (1913) who suggested that the species was synonymous with *M. spectabilis*.

The reported length with wings (35 mm.) is shorter than that of *M. spectabilis* (42 mm.). Otherwise the descriptions are insufficient to separate the species. In both, the pronotum is described and figured as wide. Without direct examination of specimens, I feel unable to evaluate critically the taxonomic status of the species, so am tentatively leaving it where it has been placed by recent authors. Possibly *M. insignis* may ultimately be shown to be a synonym of *M. spectabilis*.

SUMMARY

The nomenclature of the homologous veins and parts of the wings of the Mastotermitidae is reviewed and compared with that of the orthopteroid orders and with that of other families of the Isoptera.

Uralotermes permianus Zalessky and the family Uralotermittidae from the Permian of Russia are removed from the Isoptera and tentatively assigned to the order Protorthoptera.

Idomastotermes mysticus Haupt from the Eocene of Germany is removed from the family Mastotermitidae, but is insufficiently well known to be assigned to an order or family of insects.

Diatermes sibiricus Martynov from the Oligocene of Siberia is kept in the Isoptera but is removed from the Mastotermitidae and not assigned to any other family.

The Isoptera include six families, the Mastotermitidae, Kalotermitidae, Hodotermitidae, Rhinotermitidae, Serritermitidae, and Termitidae. The monotypic subfamily Serritermitinae Holmgren is raised to Serritermitidae, new family, with *Serritermes serrifer* (Hagen) from Brazil as type genus and species. The family Stylotermitidae Chatterjee and Thakur from India is placed in synonymy with the subfamily Stylotermitinae Holmgren of the family Rhinotermitidae.

The family Mastotermitidae Silvestri, consisting of four genera, 13 fossil species, and one living species, is reviewed. The wing venation of each genus is redescribed and compared. *Pliotermes* Pongrácz is placed in synonymy with *Mastotermes* Froggatt.

Spargotermes costalimai, new genus, new species, is described and figured from Miocene-Pliocene deposits, Minas Gerais, Brazil. The wing vena-

tion is the most primitive yet discovered in a termite.

Blattotermes neoxenus Riek from the Eocene(?) of Queensland, and *B. wheeleri* (Collins) from the Eocene of Tennessee, are redescribed and compared.

The phylogeny of an ecosystem focused around *Mastotermes darwiniensis* Froggatt, consisting of the host termite, a beetle (Staphylinidae), several species of flagellate protozoans, a spirochaete, and bacteria, is briefly discussed.

Mastotermes bournemouthensis Rosen from the Eocene of England, *M. anglicus* Rosen from the Oligocene of England, with *M. batheri* Rosen placed in synonymy, *M. heerii* (Goeppert) from the Oligocene of Germany, *M. haidingeri* (Heer) from the Miocene of Yugoslavia, with *M. vetustus* A. Pongrácz placed in synonymy, *M. croaticus* Rosen from the Miocene of Yugoslavia, with *Pliotermes hungaricus* S. Pongrácz placed in synonymy, and *M. minor* A. Pongrácz from the Miocene of Yugoslavia are each discussed and compared with other fossil species and with the single living species, *Mastotermes darwiniensis* Froggatt, from tropical Australia.

The genus *Miotermes* is questioned as a valid genus but is tentatively placed in the Mastotermitidae. *Miotermes procerus* (Heer) from the Miocene of Yugoslavia, *M. randeckensis* Rosen from the Miocene of Germany, *M. spectabilis* (Heer) from the Miocene of Germany, and *M. insignis* (Heer) from the Miocene of Germany are compared and discussed.

Maps of the world distribution of the fossil and living termites of the family Mastotermitidae are included.

ACKNOWLEDGMENTS

The unique specimen of *Spargotermes costalimai* was lent to me for study by the Divisão de Geologia e Mineralogia, Rio de Janeiro, Brazil. The British Museum (Natural History) allowed me to examine the type specimens of fossil *Mastotermes* deposited in the geological collection. The base maps used for plotting the distribution of the various genera of the Mastotermitidae are part of the Goode's Series prepared and edited by Henry M. Leppard and copyrighted by the University of Chicago Press, which granted me permission to use them. My wife, Mrs. Eleanor Fish Emerson, assisted me greatly in the preparation of the manuscript. Dr. Frank Carpenter of the Biological Laboratories, Harvard University, provided me with critical comments on the classification of fossil insects and the nomenclature of the wing veins.

BIBLIOGRAPHY

- AHMAD, M.
1950. The phylogeny of termite genera based on imago-worker mandibles. Bull. Amer. Mus. Nat. Hist., vol. 95, pp. 37-86.
- ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT
1949. Principles of animal ecology. Philadelphia and London, W. B. Saunders Co., xii+837 pp.
- ASSMANN, A.
1870. Palaeontologie. Beiträge zur Insekten-Fauna der Vorwelt. 1. Beitrag. Die fossilen Insekten des tertiären (miocenen) Thonlagers von Schossnitz bei Ranth in Schlesien. Zeitschr. Ent. Vereins schlesische Insektenk., Breslau, 62 pp.
- BANKS, N., AND T. E. SNYDER
1920. A revision of the Nearctic termites, with notes on biology and geographic distribution. Bull. U. S. Natl. Mus., no. 108, viii+228 pp.
- BATHELLIER, J.
1927. Contribution à l'étude systématique et biologique des termites de l'Indochine. In Gruvel, A., Faune des Colonies françaises. Paris, vol. 1, no. 4, pp. 125-365.
- BROWMAN, L. G.
1935. The chitinous structures in the posterior abdominal segments of certain female termites. Jour. Morph., vol. 57, pp. 113-129.
- BRUES, C. T., AND A. L. MELANDER
1932. Classification of insects. A key to the known families of insects and other terrestrial arthropods. Bull. Mus. Comp. Zoöl., Harvard College, vol. 73, pp. 1-672.
- BUGNION, E.
1914. La biologie des termites de Ceylan. Bull. Mus. Natl. d'Hist. Nat., Paris, vol. 20, no. 4, pp. 170-204.
- CALABY, J. H., AND F. J. GAY
1959. Aspects of the distribution and ecology of Australian termites. In Keast, A., R. L. Crocker, and C. S. Christian, Biogeography and ecology in Australia. Monogr. Biol., The Hague, vol. 8, pp. 211-223.
- CHANDLER, M. E. J.
1964. The lower Tertiary floras of southern England. London, British Museum (Natural History), vol. 4, A summary and survey of findings in the light of recent botanical observations, xii+151 pp.
- CHARPENTIER, T. VON
1843. Über einige fossile Insecten aus Radoboj in Croatien. Nova Acta Acad. Caes. Leopoldino-Carolinae Nat. Cur., vol. 20, pp. 399-410.
- CHATTERJEE, P. N., AND M. L. THAKUR
1963. Biology and ecology of oriental termites (Isoptera). Some observations on *Sarvaritermes faveolus* Chatterjee and Thakur (Isoptera: Stylotermidae). Indian Forester, vol. 89, no. 9, pp. 635-637.
1964. *Sarvaritermes faveolus* gen. et sp. nov. from Kulu Valley (Punjab: India) [Isoptera], with a discussion on the systematic position and relationship of the family Stylotermidae. Zool. Anz., vol. 173, pp. 149-162.
- CLEVELAND, L. R., AND A. V. GRIMSTONE
1964. The fine structure of the flagellate *Mixotricha paradoxa* and its associated micro-organisms. Proc. Roy. Soc. London, ser. B, vol. 159, pp. 668-686.

- COCKERELL, T. D. A.
- 1915. British fossil insects. Proc. U. S. Natl. Mus., vol. 49, pp. 469-499.
 - 1916. Insects in Burmese amber. Amer. Jour. Sci., vol. 42, pp. 135-138.
- COLLINS, R. L.
- 1925. A lower Eocene termite from Tennessee. Amer. Jour. Sci., ser. 5, vol. 9, pp. 406-410.
- COMSTOCK, J. H.
- 1918. The wings of the Isoptera. Chap. 8 in Comstock, J. H., The wings of insects. Ithaca, New York, Comstock Publishing Co., pp. 132-144.
- COSTA LIMA, A. DA
- 1944. Sobre dois fósseis da bacia terciaria de Fonseca (Alvinopolis-Minas Gerais). An. Acad. Brasileira Cien., vol. 16, no. 4, pp. 291-292, 1 pl.
- CRAMPTON, G. C.
- 1920. The terminal abdominal structures of the primitive Australian termite, *Mastotermes darwiniensis*. Trans. Ent. Soc. London, pp. 137-145.
 - 1922. Notes on the relationships indicated by the venation of the wings of insects. Canadian Ent., vol. 54, pp. 206-216, 222-235.
 - 1938. The interrelationships and lines of descent of living insects. Psyche, vol. 45, pp. 165-181.
- DARLINGTON, P. J., JR.
- 1964. Drifting continents and late Paleozoic geography. Proc. Natl. Acad. Sci., vol. 53, pp. 1084-1091.
- DESNEUX, J.
- 1904a. A propos de la phylogénie des termitides. Ann. Soc. Ent. Belgique, vol. 48, pp. 278-286.
 - 1904b. Isoptera. Fam. Termitidae. In Wytsman, P. A. G., Genera insectorum. Brussels, fasc. 25, pp. 1-52.
- EHRLICH, P. R.
- 1964. Some axioms of taxonomy. Syst. Zool., vol. 13, pp. 109-123.
- EMERSON, A. E.
- 1926. Development of a soldier of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) and its phylogenetic significance. Zoologica, vol. 7, pp. 69-100.
 - 1928. Termites of the Belgian Congo and the Cameroon. Bull. Amer. Mus. Nat. Hist., vol. 57, pp. 401-574.
 - 1933. A revision of the genera of fossil and recent *Termopsinae* (Isoptera). Univ. California Publ. Ent., vol. 6, pp. 165-196.
 - 1942. The relations of a relict South African termite (Isoptera, Hodotermitidae, *Stolotermes*). Amer. Mus. Novitates, no. 1187, pp. 1-12.
 - 1955. Geographical origins and dispersions of termite genera. Fieldiana: Zool., vol. 37, pp. 465-521.
 - 1961. Vestigial characters of termites and processes of regressive evolution. Evolution, vol. 15, pp. 115-131.
 - 1962. Vestigial characters, regressive evolution, and recapitulation among termites. New Delhi, UNESCO Symposium on Termites in Humid Tropics, 1960, pp. 17-30.
- ENDERLEIN, G.
- 1909. Die Klassifikation der Embiidinen, nebst morphologischen und physiologischen Bemerkungen, besonders über das Spinnen derselben. Zool. Anz., vol. 35, pp. 166-191.

FROGGATT, W. W.

1896. Australian Termitidae. Part 2. Proc. Linnean Soc. New South Wales, vol. 21, pp. 510–552.
1897a. White ants; with some account of their habits and depredations. Agr. Gazette New South Wales, vol. 8, pp. 297–300. (Reprinted in Ann. Mag. Nat. Hist., 1897, ser. 6, vol. 20, pp. 483–487.)
1897b. Australian Termitidae. Part 3. Proc. Linnean Soc. New South Wales, vol. 22, pp. 721–758.
1905. White ants (Termitidae), with suggestions for dealing with them in houses and orchards. Agric. Gazette New South Wales, vol. 16, pp. 632–656, 752–774. (Reprinted in Dept. Agr. New South Wales Misc. Publ., 1905, no. 874, pp. 1–47.)
1913. White ants. Farmers Bull. Dept. Agr. New South Wales, no. 60.

FULLER, C.

1919. The wing venation and respiratory system of certain South African termites. Ann. Natal Mus., vol. 4, pp. 19–102.

GIEBEL, C. G.

1852. Deutschlands Petrefakten. Leipzig, A. Abel, vol. 2, 706 pp.
1856. Die Insecten und Spinnen der Vorwelt mit steter Berücksichtigung der lebenden Insecten und Spinnen. Gliederthiere 1. In Fauna der Vorwelt. Leipzig, vol. 2, 18 + 411 pp.

GOEPPERT, H. R.

1855. Die Tertiäre Flora von Schossnitz in Schlesien. Görlitz.

GOLDENBERG, F.

1854. Die fossilen Insecten der Kohlenformation von Saarbrücken. Palaeontographica, Beitr. zur Naturgesch. der Vorzeit, vol. 4, pp. 17–38.

GRASSÉ, P.-P.

1949. Ordre des isoptères ou termites. In Grassé, P.-P., Traité de zoologie. Paris, Masson et Cie, vol. 9, pp. 408–544.
1952. Le fait social: ses critères biologiques, ses limites. In Structure et physiologie des sociétés animales. Paris, Colloques internationaux du Centre National de la Recherche scientifique, no. 34 [1950], pp. 7–17.

HAGEN, H. A.

- 1858a. Monographie der Termiten. Part. 2. Linnaea Ent., vol. 12, pp. 1–342, 459.
1858b. Catalogue of the specimens of neuropterous insects in the collection of the British Museum. Part 1. Termitina. London, Taylor and Francis, pp. 1–34.

HANDLIRSCH, A.

- 1906–1908. Die fossilen Insekten und die Phylogenie der rezenten Formen. Leipzig, W. Engelmann, ix + 1430 pp.
1930. Zwölftes Ordnung der Pterygogenea: Isoptera oder Termiten. In Kükenthal, W., and T. Krumbach, Handbuch der Zoologie. Berlin and Leipzig, Walter de Gruyter und Co., vol. 4, pp. 840–858.

HARE, LAURA

1937. Termite phylogeny as evidenced by soldier mandible development. Ann. Ent. Soc. Amer., vol. 37, pp. 459–486.

HARLAND, W. B., AND M. J. S. RUDWICK

1964. The great Infra-Cambrian ice age. Sci. Amer., vol. 211, pp. 28–36.

- HARRIS, W. V.**
- 1956. Colony formation in the Isoptera. Proc. Tenth Internat. Congr. Ent., vol. 2, pp. 435-440.
 - 1961. Termites. Their recognition and control. London, Longmans, Green and Co., 187 pp.
 - 1962. Classification of the phytophagous Isoptera. Symposia Genetica et Biologica Italica. Atti Congresso U.I.E.I.S., Pavia, 9-14 Settembre 1961, vol. 11, pp. 193-201.
- HAUPT, H.**
- 1956. Beitrag zur Kenntnis der Eozäne Arthropodenfauna des Geiseltales. Nova Acta Leopoldina, vol. 18, pp. 1-90.
- HEER, O.**
- 1849a. Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatiens. Zweite Abtheilung: Heuschrecken, Florfliegen, Aderflügler, Schmetterlinge und Fliegen. Leipzig, W. Engelmann, iv + 264 pp. (Termites, pp. 22-36, pls. 2-3.)
 - 1849b. In Haidinger, W., Versammlung am 5. Jänner. Ber. Mittheil. Freunden Naturwiss. Wien, vol. 5, no. 1, pp. 69-91. (Termite, p. 87.)
 - 1865. Die Urwelt der Schweiz. [Second edition.] Zürich.
- HILL, G. F.**
- 1925. Notes on Mastotermes darwiniensis Froggatt (Isoptera). Proc. Roy. Soc. Victoria, new ser., vol. 37, pt. 1, pp. 119-124.
 - 1932. Termites (white ants) in southeastern Australia. Pamphlet Council Sci. Indus. Res., Melbourne, Australia, no. 25, pp. 1-28.
 - 1942. Termites (Isoptera) from the Australian region. Melbourne, Australia, Council for Scientific and Industrial Research, pp. 1-479.
- HOLMGREN, N.**
- 1910a. Das System der Termiten. Zool. Anz., vol. 35, pp. 284-286.
 - 1910b. The Percy Sladen Trust Expedition to the Indian Ocean in 1905. No. 8, Isoptera. Trans. Linnean Soc. London, Zool., ser. 2, vol. 14, pt. 1, pp. 135-148.
 - 1911. Termitenstudien. 2. Systematik der Termiten. Die Familien Mastotermitidae, Protermitidae und Mesotermitidae. K. Svenska Vetensk.-Akad. Handl., vol. 46, no. 6, pp. 1-88.
- HOYER, B. H., B. J. McCARTHY, AND E. T. BOLTON**
- 1964. A molecular approach in the systematics of higher organisms. Science, vol. 144, pp. 959-967.
- IMMS, A. D.**
- 1919. On the structure and biology of Archotermopsis, together with descriptions of new species of intestinal Protozoa, and general observations on the Isoptera. Phil. Trans. Roy. Soc. London, ser. B, vol. 209, pp. 75-180.
- KARNY, H. H.**
- 1930. Zur Systematik der Orthopteroiden Insekten. Zweiter Teil. Treubia, vol. 12, pp. 431-461.
- KRISHNA, K.**
- 1961. A generic revision and phylogenetic study of the family Kalotermitidae (Isoptera). Bull. Amer. Mus. Nat. Hist., vol. 122, pp. 303-408.
 - 1965. Termites (Isoptera) of Burma. Amer. Mus. Novitates, no. 2210, pp. 1-34.
- LUPPOVA, A. N.**
- 1958. Termites of Turkmeniya (Turkmenistan). Ashhabad, Turkmen, S.S.R.,

- Publ. Inst. Zool. Parasit., Turkmenian Acad. Sci., vol. 2, pp. 81–144.
(In Russian.)
- McCarthy, B. J., AND E. T. BOLTON**
1963. An approach to the measurement of genetic relatedness among organisms. Proc. Natl. Acad. Sci., vol. 50, pp. 156–164.
- McKITTRICK, FRANCES ANN**
1964. Evolutionary studies of cockroaches. Cornell Univ. Agr. Exp. Sta., Mem. 389, pp. 1–197.
1965. A contribution to the understanding of cockroach-termite affinities. Ann. Ent. Soc. Amer., vol. 58, pp. 18–22.
- MARKS, E. P., AND F. A. LAWSON**
1962. A comparative study of the dictyopteran ovipositor. Jour. Morph., vol. 111, pp. 139–171.
- MARTYNOV, A.**
1929. Fossil insects from Tertiary deposits in Ashutas, Saisan district. Trav. Mus. Geol., Acad. Sci., URSS, vol. 5, pp. 173–216. (Trudy Geol. Muz. Akad. Nauk, SSSR, vol. 5 [1928–1929], pp. 173–216. (In Russian with English summary.)
1937. Wings of termites and phylogeny of Isoptera and of allied groups of insects. In N. V. Nassonov memorial volume. Moscow, Académie des Sciences de l'URSS, pp. 83–150. (In Russian with English summary.)
- NOIROT, C., AND J. KOVOOR**
1958. Anatomie comparée du tube digestif des termites. I. Sous-famille des "Termitinae." Insectes Sociaux, vol. 5, pp. 439–471.
- PONGRÁCZ, ALEXANDER**
1926. Über fossile Termiten Ungarns. Mitt. Jahrb. K. Ungarischen Geol. Anst., vol. 25, pp. 23–30.
1928. Die fossilen Insekten von Ungarn, mit besonderer Berücksichtigung der Entwicklung der Europäischen Insekten-Fauna. Ann. Hist. Nat. Mus. Natl. Hungarici, vol. 25, pp. 91–194.
1931. Bemerkungen über die Insektenfauna von Oeningen nebst Revision der Heer'schen Typen. Verhandl. Nathist.-Med. Ver. Heidelberg, vol. 17, pp. 104–125.
- PONGRÁCZ, SÁNDOR**
1917. Új harmadidöszaki termeszfaj Radobojról. A Magyar Kir. Földtani Intézet Évkönyve, vol. 25, pp. 23–36.
- RATCLIFFE, F. N., F. J. GAY, AND T. GREAVES**
1952. Australian termites. The biology, recognition, and economic importance of the common species. Melbourne, Commonwealth Scientific and Industrial Research Organization, pp. 1–124.
- REHN, J. W. H.**
1951. Classification of the Blattaria as indicated by their wings. Mem. Amer. Ent. Soc., no. 14, pp. 1–134.
- RIEK, E. F.**
1952. Fossil insects from the Tertiary sediments at Dinmore, Queensland. Univ. Queensland Papers, Dept. Geol., new ser., vol. 4, pp. 15–22.
- ROSEN, K. VON**
1913. Die fossilen Termiten: eine kürzte Zusammenfassung der bis jetzt bekannten Funde. Trans. Second Internat'l. Ent. Congr. [1912], Oxford, vol. 2, pp. 318–335.

SEEVERS, C.

1957. A monograph on the termitophilous Staphylinidae (Coleoptera). Fieldiana: Zool., vol. 40, pp. 1-334.

SHAROV, A. G.

1962. Order Paraplectoptera. In Rodendorf, B. B., Ostnovy Paleontologii. Moscow, Akademiia Nauk, vol. 9, pp. 119-134.

SILVESTRI, F.

1903. Contribuzione alla conoscenza dei Termitidi e Termitofili dell'America meridionale. Redia, Florence, vol. 1, pp. 1-234.
 1909. Isoptera. Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905, vol. 2, no. 17, pp. 279-314.
 1934. Compendio di entomologia applicata. Parte speciale. Portici, Stab. Tip. Bellavista, vol. 1, fogli 1-28, pp. 1-448. (Isoptera, pp. 27-41.)

SNODGRASS, R. E.

1952. A textbook of arthropod anatomy. Ithaca, New York, Cornell Publishing Associates, viii + 363 pp.

SNYDER, T. E.

1925. Notes on fossil termites with particular reference to Florissant, Colorado. Proc. Biol. Soc. Washington, vol. 38, pp. 149-166.
 1926. Races or sub-species in *Reticulitermes*. *Ibid.*, vol. 39, pp. 1-6.
 1949. Catalog of the termites (Isoptera) of the world. Smithsonian Misc. Coll., vol. 112, no. 3953, pp. 1-490.
 1950. The fossil termites (Isoptera) of the United States, and their living relatives. Proc. Ent. Soc. Washington, vol. 52, pp. 190-193.

STATZ, G.

1939. Gerafflänger und Wasserkäfer der oligocänen Ablagerungen von Rott. Decheniana, vol. 99A, pp. 1-102.

TILLYARD, R. J.

1926. Order Isoptera. Chap. II in Tillyard, R. J., The insects of Australia and New Zealand. Sydney, Angus and Robertson, pp. 100-106.
 1931. The wing-venation of the order Isoptera. I. Introduction and the family Mastotermitidae. Proc. Linnean Soc. New South Wales, vol. 56, pp. 371-390.
 1936. Are termites descended from true cockroaches? Nature, vol. 137, p. 655.

YU, SWETT T., AND CHENG-MING PING

1964. Studies on the faunal regions of Isoptera in China. Acta Ent. Sinica, vol. 13, pp. 10-24. (In Chinese with English summary.)

WEIDNER, H.

1955. Körperbau, Systematik und Verbreitung der Termiten. In Schmidt, H., Die Termiten. Leipzig, Akad. Verlagsgesellschaft, Geest und Portig, pp. 5-81.

ZALESSKY, G.

1937. Ancestors of some groups of the present-day insects. Nature, vol. 140, pp. 847-848.
 1939. Études des insectes permiens du Bassin de la Sylva et problèmes de l'évolution dans la classe des insectes. III. Quelques nouveaux représentants des Protohymenoptera, Homoptera, Hemipsocoptera, Psocoptera, Protopleraria, Isoptera et Protoblattoidea. Problems of Paleont., Moscow, vol. 5, pp. 33-91. (In Russian with French translation.)

ZEUNER, F.

1938. Die Insektenfauna des Mainzer Hydrobienkalks. Palaeont. Zeitschr.,
vol. 20, pp. 104–159, pls. 13–17. (Isoptera, pp. 113–117.)